HOLOTHURIANS IN THE BLUE LIAS OF SOUTHERN BRITAIN

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ABSTRACT. In a detailed study of the Blue Lias (Hettangian–Sinemurian) at four localities in southern Britain holothurian sclerites were found in 76% of samples, sometimes in abundance. There are eleven sclerite morphospecies, four of them new, including examples of the Dactylochirotida (Ypsilothuriidae), Dendro-chirotida (?Cucumariidae), Apodida (Achistridae, Chiridotidae and Synaptidae), Elasipoda and probably Molpadiida (Molpadiidae). Four types of calcareous ring are described and, where possible, their associated sclerite morphospecies identified. A number of microfossils previously assigned to the class are demonstrated to be non-holothurian including Etheridgellidae and *Rhabdotites. Calclamna* and *Binoculites* are recognized as growth stages of the same morphotype and their taxonomy revised. The fauna includes the earliest unequivocal records of the order Molpadiida and families Synaptidae and Ypsilothuriidae. New taxa are *Acutisclerus plagiacanthus* gen. et sp. nov., *Palaeoypsilus liassicus* gen. et sp. nov, *Theelia synapta* sp. nov., *Priscopedatus* sp. nov.?, and the genus *Clavallus*.

The fauna is of limited palaeoenvironmental and biostratigraphical use, although changes in size frequency (*Achistrum monochordata*) and relative abundance (*Binoculites* spp.) are potentially informative for the latter. Assemblages are difficult to recognize possibly due to taphonomic effects. The fauna is broadly similar across northwestern Europe but with regional variations both in sclerite composition and abundance.

ALTHOUGH the first fossil sclerites were described nearly one hundred and fifty years ago (Münster 1843) the study of fossil holothurians today still consists of little more than taxonomic description. This is due to the practical and taxonomic difficulties associated with fossil sclerites. Significant problems do remain concerning the classification of fossil material but there have been several monographic accounts which could provide a basis for considering holothurian palaeobiology and biostratigraphy, e.g. Croneis and McCormack (1932), Deflandre-Rigaud (1962) and Frizzell and Exline (1955). Yet there have been few references to more applied aspects such as palaeoecology (e.g. Mostler 1977), biostratigraphy (e.g. Rioult 1961; Mostler 1972c), and evolution (Pawson 1966). It therefore seemed imperative to undertake a detailed study which from the start set out to investigate the potential information obtainable from fossil holothurians. The present study is an attempt to develop such an approach and does not purport to be a definitive account of holothurians from a particular part of the stratigraphic record.

The Hettangian–Lower Sinemurian part of the Blue Lias in Britain was chosen as the subject of study for several reasons. Most importantly a number of micropalaeontologists have indicated the frequent occurrence of sclerites in this facies. Records include dumb-bell-shaped spicules from Hock Cliff (Henderson 1935) and hooks from the *planorbis, angulatus,* and *bucklandi* zones of the Yorkshire Lias (Blake 1876). In an unpublished report, Clements *et al.* (1975) noted the presence of holothurians in several samples from the Blue Lias near Rugby. In addition, the biostratigraphy of the Blue Lias is well documented and there are a number of well described and easily accessible sections available.

Liassic holothurians are also widely known from other parts of Europe, particularly Germany (Issler 1908; Bartenstein 1936; Bartenstein and Brand 1937; Mortensen 1937; Kristan-Tollmann 1986). In France early records included Terquem (1862) and Terquem and Berthelin (1875). Later Rioult (1961) described sclerites from the Lias of Normandy and discussed their possible use in biostratigraphy. Michelson (1972) provided an excellent account of palaeoecology and

morphological variation of holothurian (and ostracod) assemblages from the Lias of the Danish Embayment.

METHODS

Sampling

Hand-sized samples were collected from logged sections at Pinhay Bay (P), near Lyme Regis, SY 320908; Hock Cliff (H), on the River Severn, at SO 726091; Maisemore Cliff (M), also on the Severn, at SO 812216; and Long Itchington quarry (L), near Rugby, SP 419631. Throughout the text sample numbers are prefixed by P, H, M, or L depending on locality. E numbers are British Museum (Natural History) catalogue numbers.

Processing

Several extraction techniques were applied to identical test samples for evaluation. Decanting of disaggregated samples, as recommended by Frizzell and Exline (1955), was not successful. The following method proved the best since samples could be processed relatively quickly and the majority of the material isolated remained well preserved. A hand-sized sample was broken into 0·5 cm fragments, dried in an oven, immersed in kerosene for 30 minutes and, after decanting off the kerosene, immersed in boiling water and left for 1·5–2 hours. The resultant sludge was gently washed through 0·5 cm and 63 μm (240 mesh) sieves with water and a little detergent and dried in an oven. The dried residue was immersed in 10% hydrogen peroxide for 30 minutes, washed through the 63 μm sieve again and dried. A small proportion of the final residue was removed and further cleaned in an ultrasonic tank for 15 seconds. To prevent cross-contamination of samples, all equipment was kept thoroughly clean including dislodging unwanted material from the fine sieve with a powerful jet of water.

Picking

The residue was lightly scattered over an 8 × 7 cm tray and scanned/sorted under a binocular microscope. Microfossils were transferred and stored on gum-coated Franke slides. In order to determine the relative abundance and co-occurrence of morphotypes the numbers of each type of sclerite were recorded from four 'pickings'. In addition material treated ultrasonically was scanned for excellent specimens.

Most of the measurements were made with a graticule eyepiece binocular microscope. For scanning electron microscopy, spicules were mounted on photographic film, and larger material with 'Evostick' wood glue. These were coated with gold palladium and observed with Hitachi S-2500, Cambridge 100 and Cambridge 180 scanning electron microscopes.

SCLERITE DISTRIBUTION IN THE BLUE LIAS

Occurrence of sclerites

Sample details and numbers of various sclerite types are shown in Text-figures 1–2. Of the 110 samples processed 76% contained holothurian sclerites, some in abundance (> 50 from four pickings). In the remaining 26 samples 23 had few or no other microfossil elements. No relationship could be discerned between the presence or abundance of holothurians, or particular morphotypes, with any other group of microfossils which included echinoid, ophiuroid, asteroid and crinoid debris, ostracods, foraminiferans, bivalves, microgastropods, sponges and fish fragments. Rioult (1961) noted that holothurians were numerous in beds rich in other echinoderms but variable compared with ostracods and foraminiferans. Michelson (1972) reported the co-occurrence of the ostracod genus *Macrocypris* with the highest abundance of holothurian sclerites but an inverse relationship with the genus *Lophocythere*. In the present material non-holothurian components of the microfauna were not studied in such taxonomic detail but no correlation was observed between holothurian abundance and the distribution of different ostracod types.
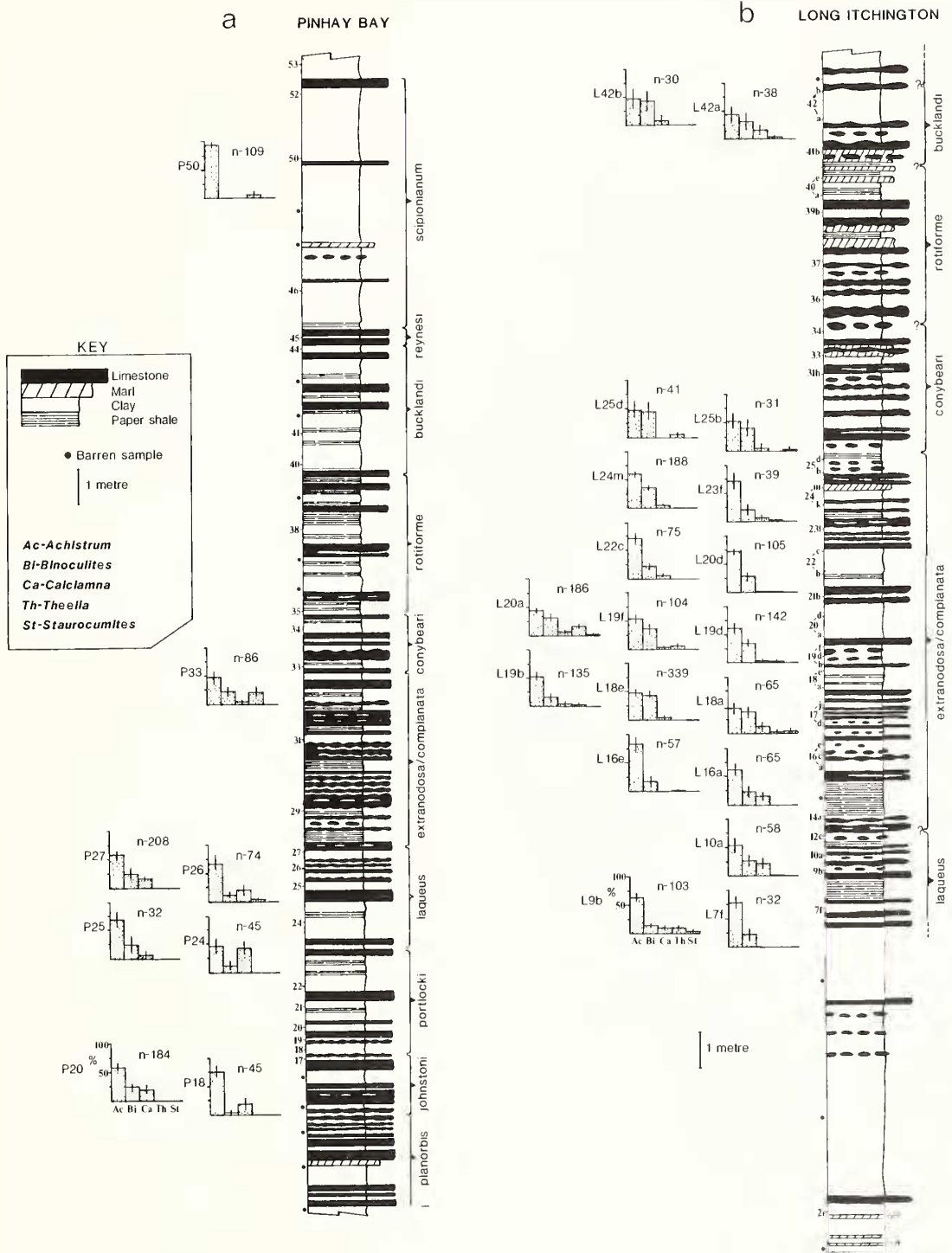
TEXT-FIG. 1. *a*, Section through the Blue Lias at Pinhay Bay. *b*, Section through the Blue Lias at Long Itchington. Sample numbers used at Long Itchington are after Clements *et al.* (1975). Sections shown with reference to ammonite subzones. Numbers on section are samples; sample numbers on the histograms preceded by P (Pinhay Bay) or L (Long Itchington). Histograms record the relative abundance (mean ± 2 standard errors) of each major morphotype from samples with a total sclerite complement (*n*) of 30 or more (after '4 pickings').
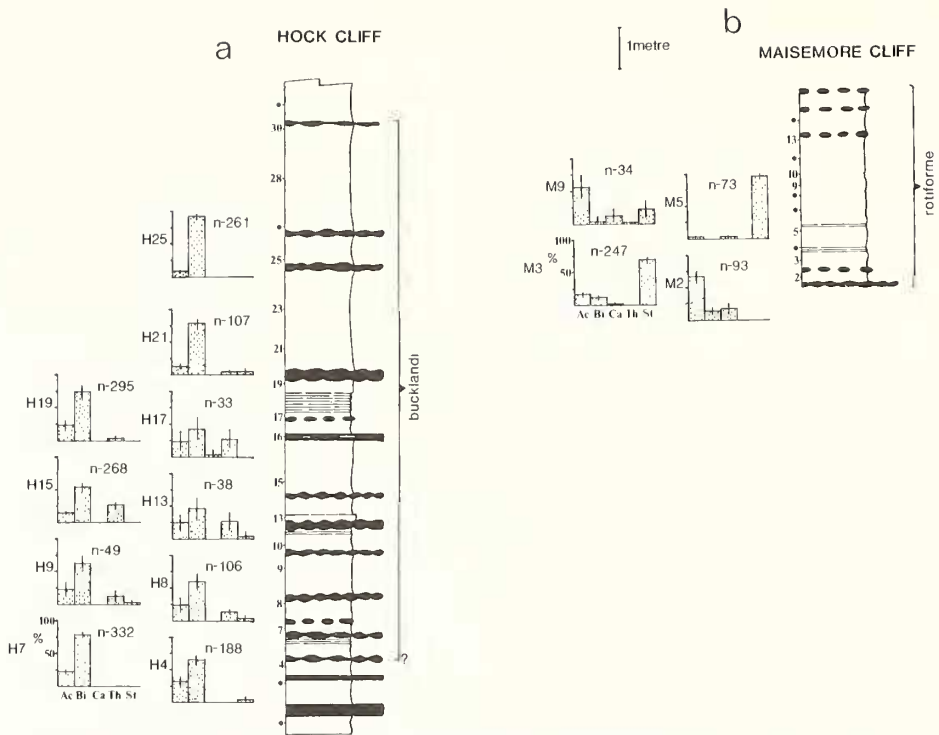
TEXT-FIG. 2. *a*, Section through the Blue Lias at Hock Cliff. *b*, Section through the Blue Lias at Maisemore Cliff. Sections shown with reference to ammonite subzones. Numbers on section are samples; sample numbers on the histograms preceded by H (Hock Cliff) or M (Maisemore Cliff). Histograms record the relative abundance (mean ± 2 standard errors) of each major morphotype from samples with a total sclerite complement (*n*) of 30 or more (after '4 pickings').
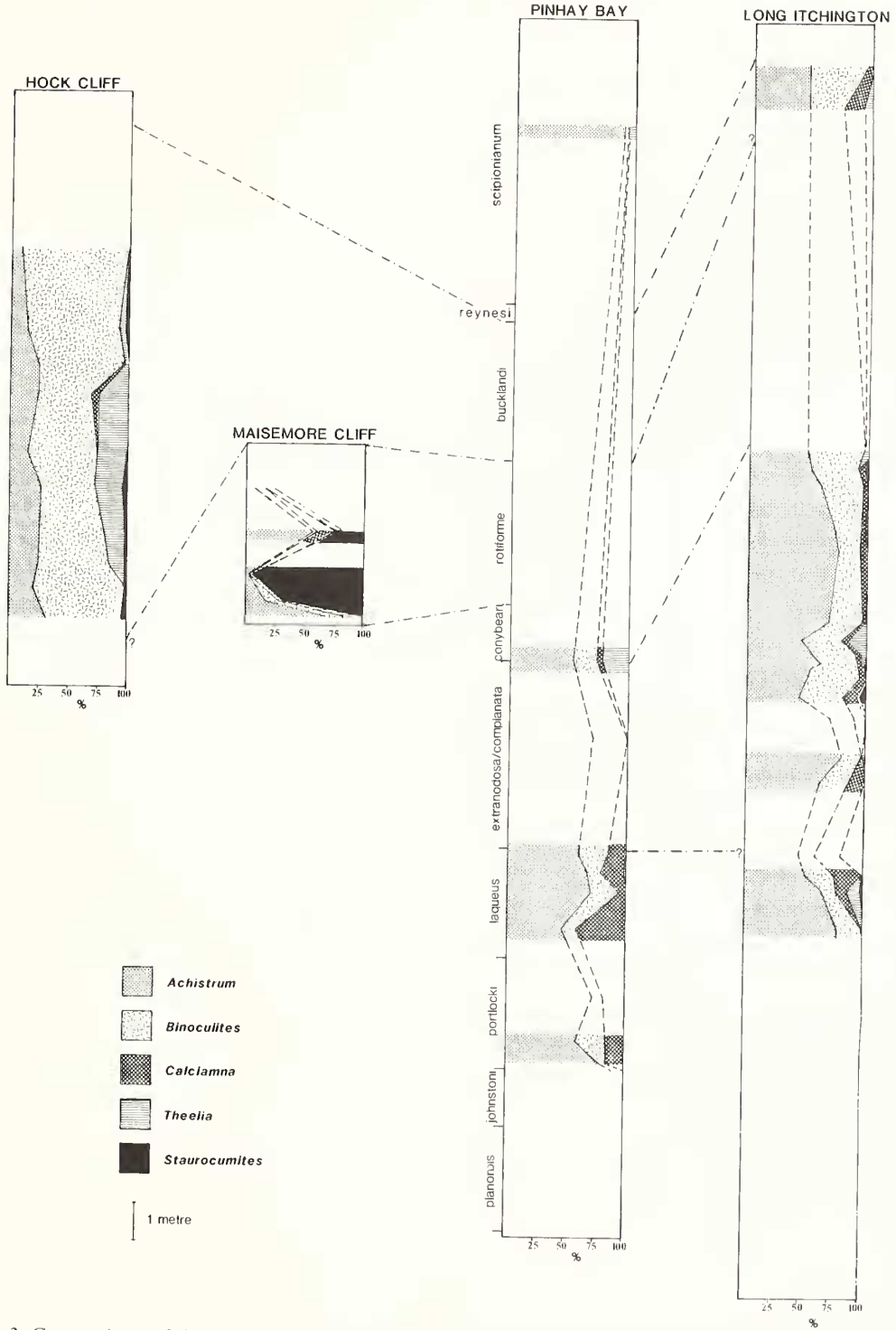
Sclerite abundance

An estimate of the numbers of sclerites per weight of sediment from L18*e*, the most holothurian rich sample, gave an equivalent of 12250 per 100 g, comparable with the number of ostracod valves. An average figure nearer 4000 sclerites/100 g was calculated for samples in which sclerites were relatively common, i.e. those shown in Text-figures 1–2. This is still significantly higher than the maximum value of 400 sclerites/100 g given by Michelson (1972).

Composition and sclerite association

The most conspicuous elements of the holothurian fauna are 'hooks' – *Achistrum monochordata* Hodson, Harris and Lawson, 'dumb-bells' – genus *Binoculites* Deflandre-Rigaud, 'plates/buttons' – genus *Calclamna* Frizzell and Exline, 'wheels' – genus *Theelia* Schlumberger, and 'tables' – *Staurocumites bartensteini* Deflandre-Rigaud.

The relative numbers of the main morphotypes were recorded to determine whether two or more consistently co-occurred and thus might be considered to form a sclerite assemblage (see Gilliland 1990, Section 2.2.2). For example, if hooks and wheels were possessed by the same species one would expect both to occur in the same samples. A constant ratio between components of an assemblage cannot be assumed. On the other hand an increase or decrease in one morphotype should, at least, be accompanied by a similar change in the other morphotypes, and this should be observable in fossil material.

The relative abundance of sclerites from each section is summarized in Text-figure 3. There is no

TEXT-FIG. 3. Comparison of the relative abundance of the main morphotypes within each section using Pinhay Bay as a reference for correlation (dot-dash lines). Shaded areas are parts of the section with samples containing 30 or more sclerites. Dashed lines indicate extrapolation between the shaded areas but with information included from samples with between 20 and 30 sclerites.

evidence of an association between any of the five major morphotypes. For example, *Staurocumites bartensteini* has a sporadic distribution which does not relate to any of the other four morphotypes and *Binoculites* occurs at Hock Cliff without the presence of *Calclamna*. *Binoculites* generally changes inversely to *Achistrum*, and there is no correlation between the latter genus and *Theelia*.

The relative abundance of morphotypes is useful for constructing a 'faunal profile' within and between sections. This is constructed from the number of discrete sclerites within a standard sample size, but, unfortunately, cannot be related to numbers of individual animals since a *Staurocumites*-bearing species may have more sclerites per individual than an *Achistrum*-bearing species. Similarly, changes in the relative numbers of morphotypes could represent changes in the density of sclerites within a species or between populations. Therefore it cannot be assumed that the predominance of a morphotype is indicative of a dominant species in the living holothurian fauna. Post-mortem sorting of different sclerites is probably not significant (see discussion).

There are some changes within the sections (Text-fig. 3), but, given the sporadic occurrence of sufficient numbers of specimens, particularly from the same periods of time at different sections, little correspondence between sections can be recognized. It is difficult to explain why there are incongruities in the absolute abundance of sclerites: there are no consistent differences in the lithology or associated microfauna of samples in which holothurians are common and those in which they are not.

Whilst faunal/sclerite composition offers little stratigraphic use, broad trends within sections are worth comparing. Sclerite composition during the Upper Hettangian is similar in the Pinhay Bay and Long Itchington sections, i.e. a predominance of *Achistrum*, a significant proportion of *Binoculites*/*Calclamna*, and a sporadic occurrence of *Theelia* and *Staurocumites*. Further up the section in the *bucklandi* zone at Long Itchington the percentage of the various sclerites remains similar to the lower part of the section. However, at Pinhay Bay, in the *scipionianum* subzone, the composition changes significantly and hooks become more important. At Hock Cliff the situation differs with *Binoculites* (and only a few *Calclamna*) more significant than *Achistrum* and more wheels compared to other localities. The composition at Maisemore Cliff is strikingly different with marked fluctuations in *Staurocumites*, a morphotype which is rare or absent in the other sections. Hence, in spite of the limited data there appears to be evidence of greater geographical than stratigraphic variation.
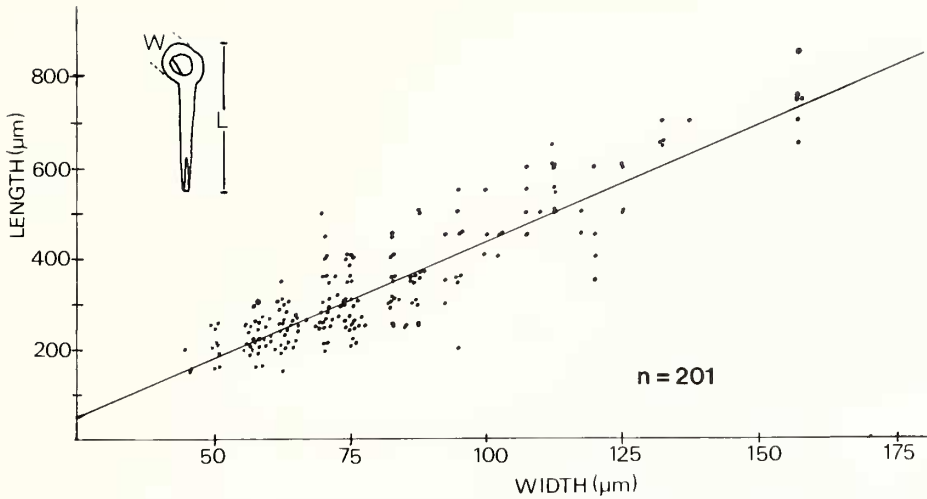
VARIATION OF *ACHISTRUM MONOCHORDATA*

Hooks occur throughout the sections studied and are commonly the most conspicuous type of sclerite (see Text-figs 1–2). All of the hooks can be referred to *Achistrum monochordata*. The morphospecies is present in sufficient numbers to allow an analysis of changes in its morphology.

Initial observations indicated that only size and eccentricity (whether the head lies to the right or left of the shaft) varied appreciably. Most hooks are broken along the shaft so head width was used as a parameter of size, since in intact hooks width correlates well with length (Text-fig. 4). Fifty specimens were picked from samples in which *A. monochordata* was relatively common or abundant. A comparison of the measurements of two sets of fifty hooks from the same sample (L18*e*) gave an insignificant difference in width ($t = 0.7$ compared with the tabulated value of $t = 1.658$, at $P = 0.05$).

The ratio of left to right 'headed' hooks varied between 0.515 (L24*m*) and 1.941 (L16). There is no evidence of a relationship between this variation and variation in hook size (the correlation coefficient value for left:right ratio against mean width is 0.04). Indeed the mean widths of left and right hooks are almost identical – left = 106.5 μm, $n = 554$, right = 106.8 μm, $n = 592$, with 4 examples showing no eccentricity. Both left and right hooks occur in the body wall of whole body individuals from the Carboniferous Mazon Creek locality (personal observation).

A change can be seen in hook size over time (Text-fig. 5). All the means from the cluster of high values in the *portlocki–conybeari* period are significantly different from those of the *rotiforme–reynesi* period (at the $P = 0.05$ level) except the 'largest' value of the lower cluster (lower *rotiforme*) and the

TEXT-FIG. 4. A plot of length against width of head in *Achistrum monochordata*. The regression equation is Width = 14·7 + 0·1938 Length; R^2 = 79·2%, correlation coefficient = 0·891.
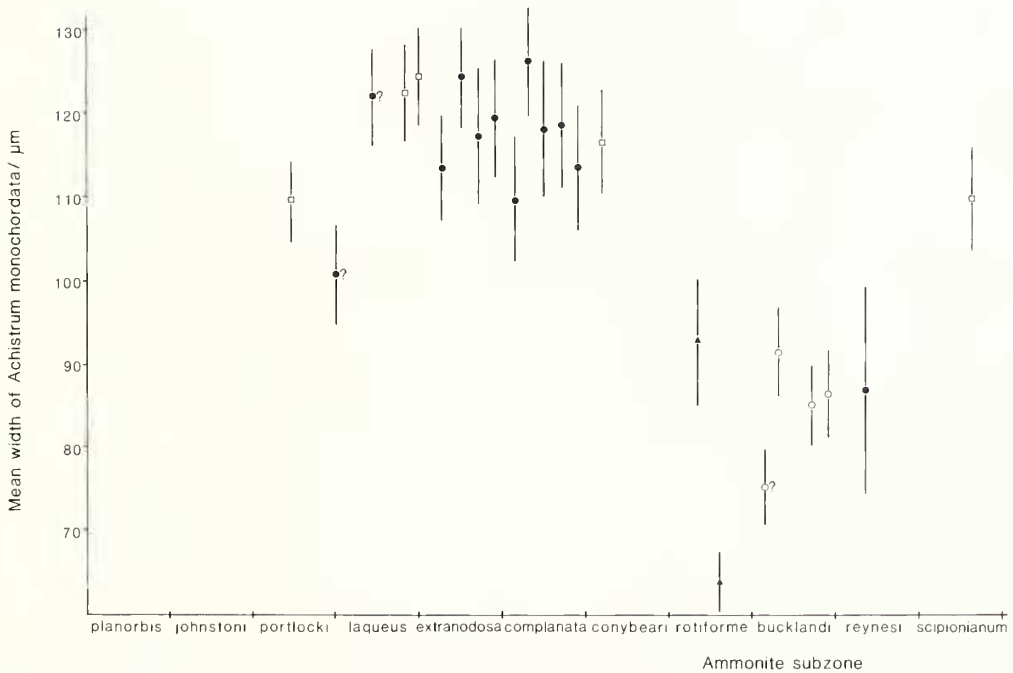
TEXT-FIG. 5. Values of mean width (± 2 standard errors) of *Achistrum monochordata* ($n = 50$) from various samples through the Blue Lias. Question marks indicate samples of uncertain stratigraphic age. $\square$ = Pinhay Bay, ● = Long Itchington, ○ = Hock Cliff, ▲ = Maisemore Cliff.

'smallest' value of the higher cluster (upper *portlocki*). The variation appears to be over time rather than between localities (i.e. geographical variation) because samples from Long Itchington occur in both the main groups of values.

The possible cause(s) of the observed trend in hook size are not obvious. Nothing is known about the size of hooks, or analogous Recent sclerites, compared with the size of the individual animal, and it is difficult to envisage a link between the average spicule size and any environmental factors. Post-mortem effects such as sorting can be dismissed because there is no consistent correlation between width frequency distribution and mean size (see Text-fig. 6a–e). The observed change in
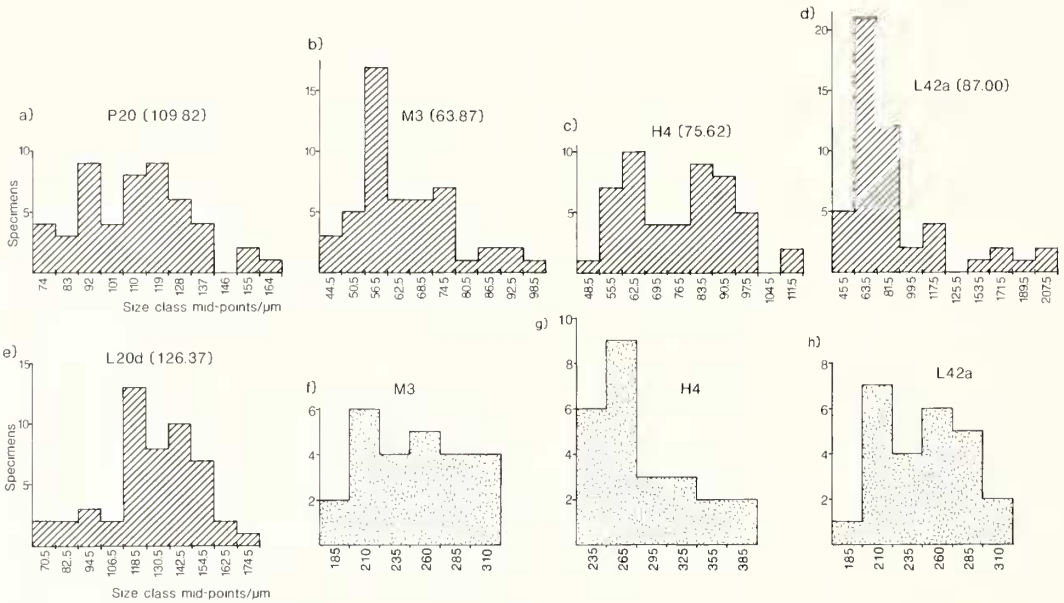
TEXT-FIG. 6. *a–e*, Size frequency histograms of the head width in 50 specimens of *Achistrum monochordata* from selected samples. Figure in brackets is the mean width. *f–h*, Size frequency histograms of length in 25 specimens of *Binoculites terquemi* from selected samples.

Figs 1–7, 9, 20. *Binoculites terquemi* Deflandre-Rigaud. 1, E27320; H9; *bucklandi* subzone, × 105. 2, E27313; H4; *bucklandi* subzone, × 110. 3, E27321; H9; *bucklandi* subzone, × 40. 4, E27324; L10a; *laqueus? extranodosa/complanata* subzone, × 90. 5, E27330; L10a; *laqueus?extranodosa/complanata* subzone, × 115. 6, E27296; L9b; *laqueus?extranodosa/complanata* subzone, × 110. 7, E27279; L10a; *laqueus?extra-nodosa/complanata* subzone, × 155. 9, E27315; L10a; *laqueus?extranodosa/complanata* subzone, × 205. 20, E27344; H7; *bucklandi* subzone, × 70.

Figs 8, 12–17. *Binoculites jurassica* Frizzell and Exline. 8, E27289; L9b; *laqueus?extranodosa/complanata* subzone, × 105. 12, E27317; L10a; *laqueus?extranodosa/complanata* subzone, × 100. 13, E27291; L18e; *angulata* zone, × 95. 14, E27292; L18e; *angulata* zone, × 95. 15, E27293; L18e; *angulata* zone, × 95. 16, E27294; L18e; *angulata* zone, × 95. 17, E27305; L24k; *angulata* zone, × 95.

Figs 10–11. *Eocaudina*-type plates. 10, E27360; L33b; *conybeari?rotiforme* subzone, × 115. 11, E27335; H13; *bucklandi* subzone, × 145.

Figs 18–19. *Frizzellus*-type elements. 18, E27404; P27; *laqueus* subzone, × 120. 19, Disc scale of the Recent ophiuroid *Amphilepis norvegica*; from 300 m depth; Trondljemsfiord, Norway, × 120.

Figs 21–22. *Rhabdotites?rectus* Hampton. E27042; Upper Bathonian; Dorset, × 230, × 100, respectively.

H, L, M and P numbers refer to samples. E numbers are British Museum (Natural History) catalogue numbers.

PLATE 1
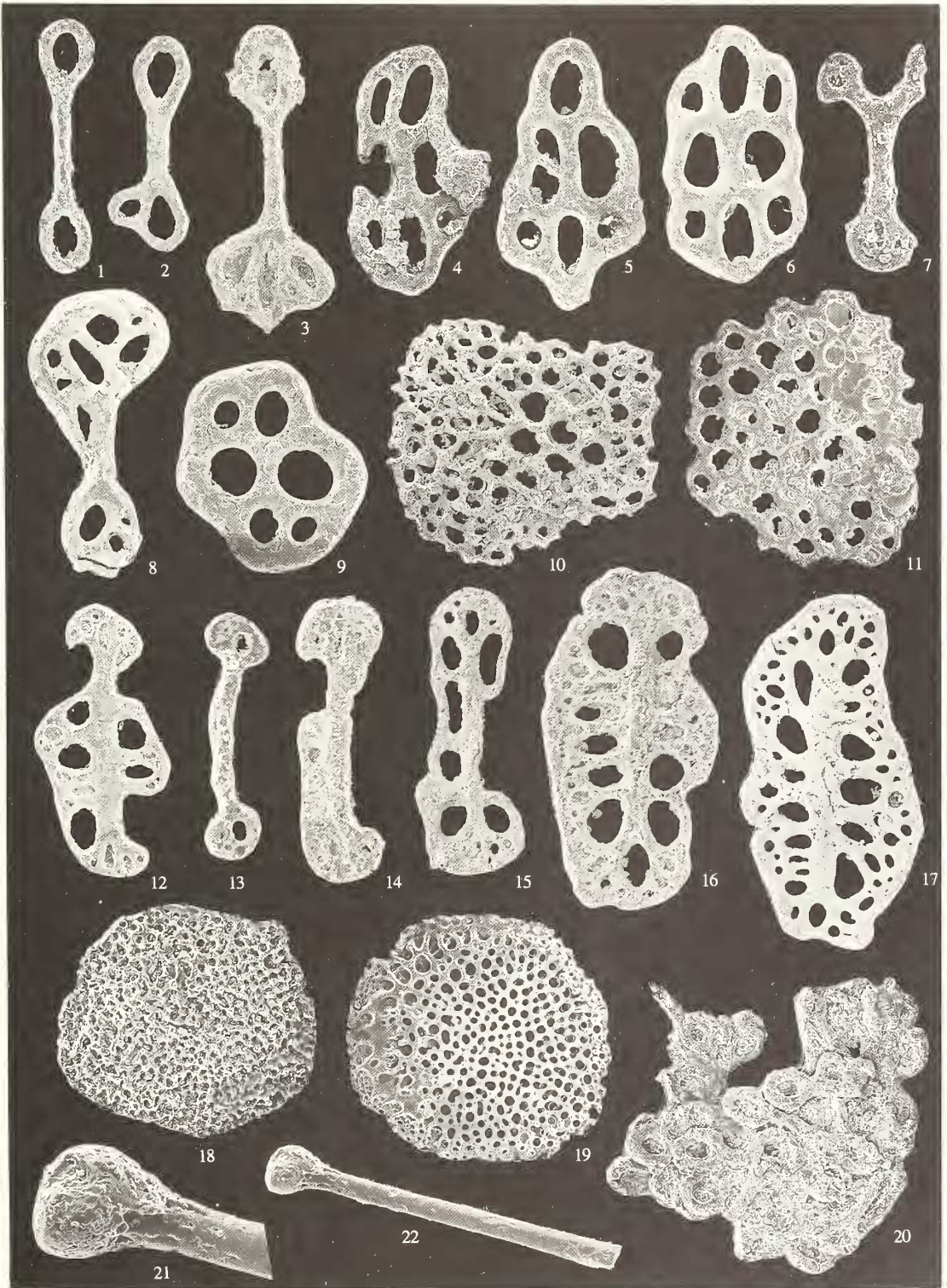
GILLILAND, Blue Lias holothurian sclerites

size may have stratigraphic application but the small size of samples in some parts of the succession makes this difficult to prove. In addition there is a possible cycle of increasing/decreasing size, but this also cannot be confirmed because of the low frequency of hooks in the critical period prior to the *portlocki* subzone.

THE MORPHOGENERA *BINOCULITES* AND *CALCLAMNA*

Dumb-bell-shaped sclerites of the genus *Binoculites* Deflandre-Rigaud are common in the material studied. Three 'species' occur distinguished on the number of holes in the expanded ends (Rioult 1961): *B. terquemi* Deflandre-Rigaud (one hole), *B. irregularis* Frizzell and Exline (< five) and *B. issleri* Deflandre-Rigaud (> five). On the basis of the present material the three taxa are intergradational and can no longer be separated; there are even examples with a different number of holes at either end that could be classified as one of two different 'species' depending on which end is selected (Pl. 1, figs 2–3).

Observations of over 1500 specimens indicate that *Binoculites* and plates/buttons of the genus *Calclamna* are linked in a morphological growth series with the former developing into the latter. However, it is possible that some of the apparent 'early growth stages' had completed growth, i.e. within one individual there was a mixture of *Binoculites*, perhaps restricted to one part of the body such as the tube-feet, together with *Calclamna* at all stages of formation.

Two different growth series are evident, each derived from a different form of *B. terquemi*. The first, here referred to as '*Calclamna* group one', begins with a short *B. terquemi* with relatively wide terminal holes (*B. terquemi* form *beta* of Rioult 1961). Additional holes are added at each end commonly before development of the central holes. Subsequent growth from each end of the 'dumb-bell' and outwards from the shaft produces a cruciform pattern of holes. The 'end product', *Calclamna germanica*, is variable in shape, and the number, size and distribution of the additional holes are also variable. Occasionally a 'bar' has grown across and divided one of the central holes (Pl. 1, fig. 5). Michelson (1972) noted a similar variation in *Calclamna germanica*, but a bar was more frequent in his material.

The second growth series, '*Calclamna* group 2', begins with a relatively long and thin *B. terquemi* (form *gamma* of Rioult 1961). This form can usually be identified by the thickness of its shaft, which is nearly as thick as the two ends, and, except in smaller specimens, by a greater length/width ratio (see Text-fig. 7), although a distinction between the two forms of *B. terquemi* cannot always be made. Due to the long shaft section of *B. terquemi* form *gamma* subsequent growth creates two rows of holes along the length of the shaft. The formation of bars is obvious in some specimens and contributes to an increase in the number of central holes. Sometimes the middle part has fully formed before the rest of the sclerite, resulting in the morphospecies *Calclamnella jurassica* Frizzell and Exline (Pl. 1, fig. 12). At the periphery there are many small holes which occur rarely in *Calclamna germanica* (Pl. 1, fig. 17). In a number of examples of '*Calclamna* group two' the central shaft and rim of the plate are thicker than the rest of the sclerite.

Elongate plates with two rows of holes are normally included in the morphogenus *Calclamnella* Frizzell and Exline. Here *Calclamnella* is restricted to elongate plates with two rows of holes which lack the terminal holes that are characteristic of *Calclamna*. This distinction is important because the buttons/plates of dendrochirotes are like *Calclamna*, whereas the buttons of aspidochirotes are usually like *Calclamnella* as defined here.

The two growth series result in apparently different morphologies (compare Pl. 1, fig. 6 with fig. 17), but do these represent distinct biological taxa? The formation of bars, increasing hole number, and the occurrence of intermediate forms (Pl. 1, figs 7–8) serve to reduce the distinction between the two series. In the material of Michelson (1972) the proportion of intermediates was evidently quite high. On the other hand the range of variation represented by the two series is not known in any one Recent species. Thus the morphological evidence may indicate two distinct biological species, but is there supporting evidence from their stratigraphic distribution?

The stratigraphic distribution of the two groups offers conflicting evidence. Both types are known
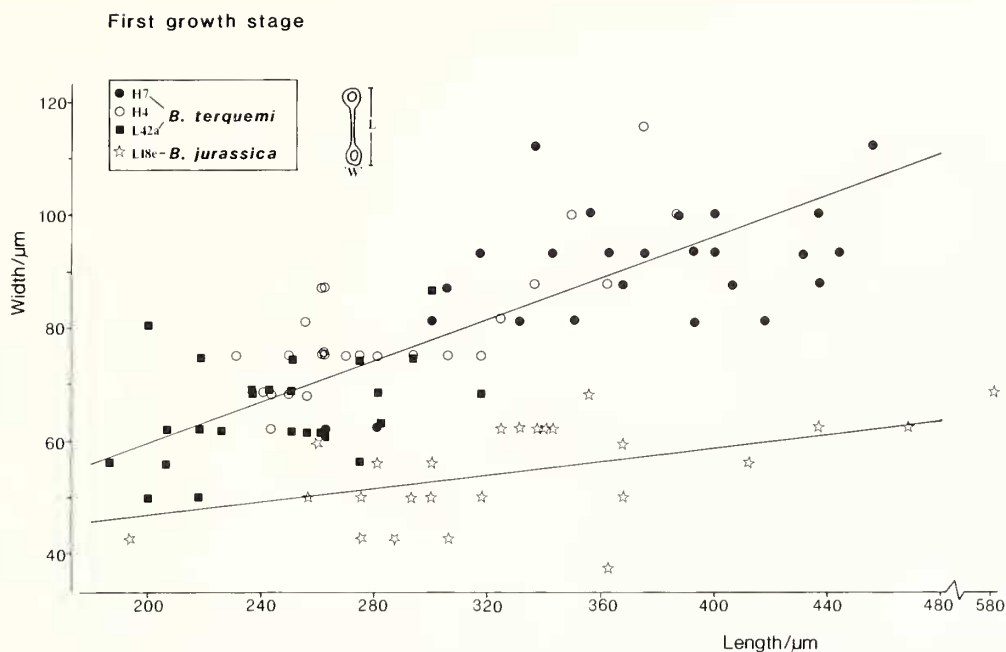
First growth stage

TEXT-FIG. 7. Plot of length (L) against width (W) of the earliest growth stage for *Binoculites terquemi* (regression equation: Width = 23·75 + 0·18 Length) and *B. jurassica* (W = 35·34 + 0·06 L), *n* = 25 for each sample (see text for discussion of taxonomy).

from the Middle Triassic upwards and have been recorded together (e.g. Issler 1908; Michelson 1972; Gupta and Kachroo 1976; Gheorghian 1976). In this study they have a similar overall stratigraphic range (Text-fig. 8), and in most samples there are specimens from both groups. The relative proportions of each group, however, vary stratigraphically (Text-fig. 8). In the *portlocki–laqueus* subzones there is a mixture of both *Calclamna* groups, followed by an increase in the proportion of 'group two' and then, towards the top, there is almost complete dominance of 'group one'. Within each group the ratio of *Binoculites* to *Calclamna* is markedly different in the lower part of the section, even in the same sample. In the *rotiforme/bucklandi* subzones, at Hock Cliff and Maisemore Cliff, 'group one' is composed almost entirely of *Binoculites terquemi* of variable size which may even represent a third 'group'. Assemblages from the same period at Long Itchington, however, retain the full growth series and resemble those from lower down in the section.

Thus the differences between all stages of each growth series and the quantitative stratigraphic evidence suggest a distinction between two species, whereas the occurrence of sclerites intermediate between both growth series and the gross stratigraphic distribution suggest there is only one species. However, the degree of variation represented by the two series is greater than that known from any Recent species. The two groups are therefore separated as two closely related 'biological' species.

The following taxonomic revision is proposed. The *Binoculites* of each species (growth series) can be distinguished as described above. The final stage of 'group one' is *Calclamna germanica* and of 'group two' *Calclamna jurassica*. Both growth series belong to the same genus for which the senior synonym is *Binoculites*. Each growth series must be named after the senior specific synonym within each, i.e. *Binoculites terquemi* and *Binoculites jurassica* respectively. The morphotypes 'Binoculites' (= early growth stage), restricted to those sclerites which have not yet lost the distinctive dumb-bell shape, and 'Calclamna' (= late growth stage) are retained as informal names in order to identify possible significant (geographical/evolutionary?) changes in the ratio of these two stages. For
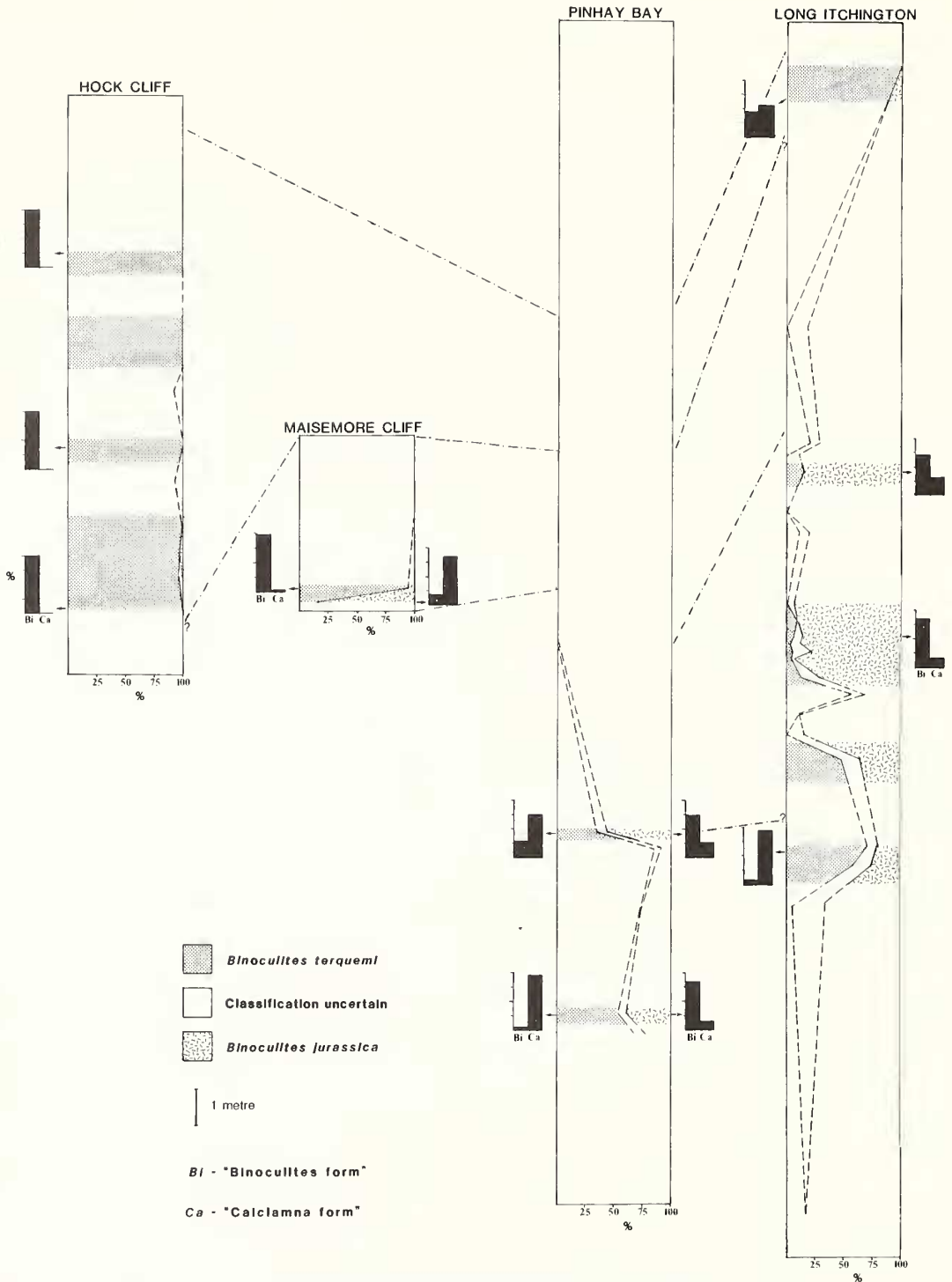
TEXT-FIG. 8. Comparison of the relative occurrence of the two *Binoculites* species (see text for discussion of taxonomy). Shaded areas are parts of the section with 25 or more 'Calclamna/Binoculites' sclerites. Histograms indicate the percentage of the two forms 'Binoculites' and 'Calclamna' among the sclerites of each species. Correlation as for Text-figure 3.

example, Michelson (1972) recorded very few specimens of the form Binoculites amongst more than 1700 of the form Calclamna from the Lias of the Danish Embayment. The high percentage of early growth stages at Hock Cliff and Maisemore Cliff is interpreted as geographical variation within the species *Binoculites terquemi*.

ELEMENTS OF THE CALCAREOUS RING

A significant number of elements of the calcareous ring were recovered from the Blue Lias. Fossil records of elements of the calcareous ring are remarkably rare considering the number of described sclerites (Gilliland 1990, Section 5.4). The descriptive terminology used for the gross structure is based on that of Belyaev and Mironov (1977) as outlined in Gage and Billet (1986). Two main types of ring, and two others, can be distinguished.

Calcareous ring Type 1

More than twenty specimens each of radial (Pl. 5, figs. 6–10; Pl. 6, fig. 1; Text-fig. 9*f*–*g*) and interradial (Pl. 5, figs. 3–5; Text-fig. 9*d*–*e*) elements were found (including BMNH E27415–27419, E27424–27425, E27428, E27439, E27441–27442), from the *extranodosa/complanata, rotiforme* and *bucklandi* subzones.

Interradials. The anterior end consists of a well-developed pointed process, relatively large lateral crests and associated small frontal excavations. The whole element tends to be curved with the inner face being concave and the lateral articulation faces inclined inwards (Pl. 5, fig. 3). Associated with the posterior indent is a sunken area on the inner face which shallows anteriorly (Text-fig. 9*e*). The stereom is typically very dense with thickened trabeculae and small pores (diameter *c*. 10–15 μm) over a large part of the outer face (Pl. 5, fig. 5) but may be comprised of a more open labyrinthic stereom, as in the rest of the outer face and the entire inner face, or a denser, 'knobbly' stereom as on the frontal excavations (Pl. 5, fig. 5).

Radials. There are one or two anterior processes. The first, found in most specimens, is short and broad with a central notch (e.g. Pl. 5, figs 8, 10). The additional process is longer and pointed like that of the interradial (Pl. 5, fig. 8). On the external face a depression lies posterior to the notch of the broader process and, when present, between the two anterior processes. Compared to the interradials, the radials are more elongate, less curved (internally/externally), and the posterior indent may be deeper, but the lateral crests and frontal excavations of both elements are similar. On the inner face the posterior indent extends into a furrow which divides anteriorly into two or three branches (Pl. 5, fig. 7; Text-fig. 9*f*). The stereom resembles that of the interradial but is consistently more dense on the main part of the external surface (Pl. 5, fig. 8).

Discussion. Although these elements are quite variable they are closely comparable with the calcareous ring elements found in the order Molpadiida. In fact variation in the shape of the Type 1 elements is not unusual in Recent species, where it merely reflects the relative position within the calcareous ring (Hatanaka 1939). The relative length of interradials is also known to vary with age (Hozawa 1936). Hess (1975) described similar examples from the Oxfordian of Switzerland which he also assigned to the Molpadiida.

By comparison with Recent material it is possible to infer some of the soft tissue components of the fossil material. The longitudinal muscle would have inserted onto the notched anterior process of the radial piece (see Text-fig. 9*f*). The furrow would have housed the anterior extension of the radial canal. This normally divides into three tentacular canals (leading to a total of fifteen tentacles from five radials in Recent molpadiids) and a much smaller radial canal. In the fossil material details of this part were not observed, possibly because the furrow was very shallow and the reduced section of the radial canal may have been too small to have left a preservable trace. Hence it is unfortunately not possible to infer the number of tentacles present in this species. The reduced part of the radial

canal would have passed over the front of the radial through the notch of the main anterior process.

Of the four families of Molpadiida the calcareous ring described here is most likely to be derived from the Molpadiidae. In this family the radial elements possess a single posterior process, which is commonly notched, and, in some species, a notch in the anterior process for the passage of the radial canal and nerve. The radial elements of the Caudinidae also have a notch on the anterior process but, by contrast, there are large posterior prolongations (see Heding 1935). The ring elements of the Gephyrothuriidae are different, being short and very broad with anterior ridges rather than processes (Heding 1935). In the Eupyrgidae the posterior process is rudimentary and there is a perforation, rather than a notch, for the passage of the radial canal and nerve (Heding 1935).

Calcareous ring Type 2

More than 25 specimens were recorded, including BMNH E27420–27423, E27440 (Pl. 6, figs 2, 4–5, 8–10; Text-fig. 9a–c), from the *laqueus?extranodosa/complanata*, *extranodosa/complanata*, *conybeari*, *rotiforme?bucklandi* and *bucklandi* subzones. The radial and interradial elements are very similar in structure and cannot be differentiated.

There is one, or occasionally two (Pl. 6, fig. 10), prominent anterior process with a well-developed central crest which also projects from the inner face (Pl. 6, fig. 5). The lateral crest, or ridge, is
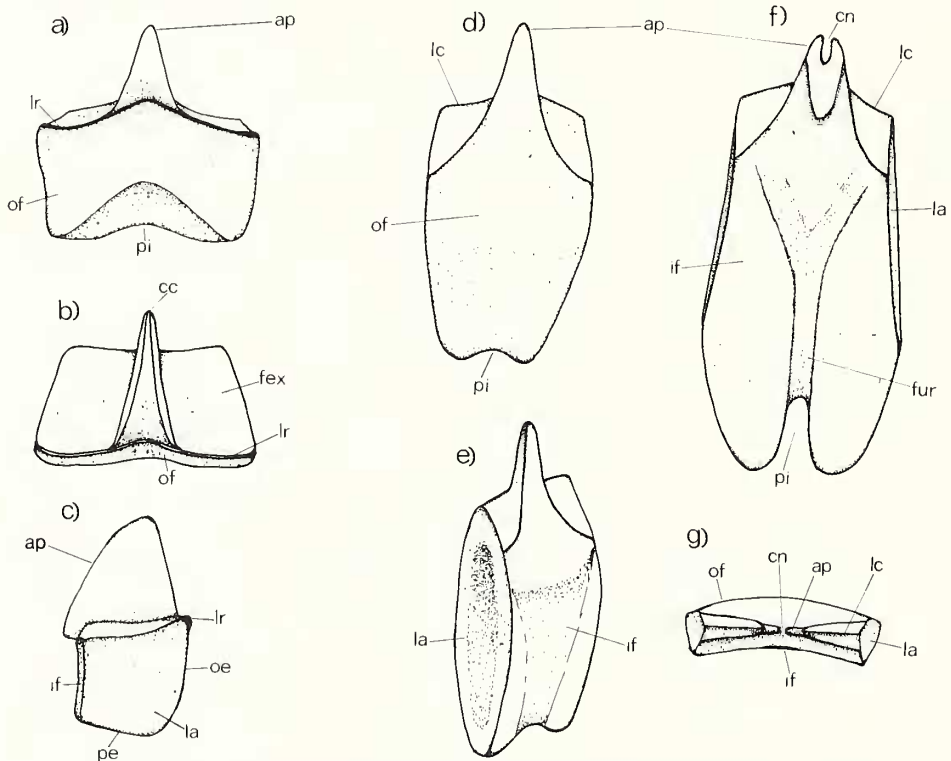
TEXT-FIG. 9. *a–c*, reconstruction of calcareous ring Type 2, example with one anterior process; *a*, outer face; *b*, lateral view; *c*, anterior view. *d–g*, reconstruction of calcareous ring Type 1; *d*, interradial, outer face; *e*, interradial, oblique view of inner face; *f*, radial, inner face; *g*, radial, anterior view. Abbreviations: ap, anterior process; cc, central crest; cn, central notch; fex, frontal excavation; fur, furrow; if, inner face; la, lateral articulating face; lc, lateral crest; lr, lateral ridge; oe, outer edge; of, outer face; pe, posterior edge; pi, posterior indentation.

usually well developed (Pl. 6, fig. 4). The frontal excavations are relatively large and flat (Pl. 6, fig. 4) as are the lateral articulation faces. The posterior end is slightly concave or indented except in one example in which there is a well-developed process (Pl. 6, fig. 9). The internal face, and sometimes the external face, may be deeply sunken near the posterior edge and shallows to form a ridge anteriorly (Pl. 6, fig. 2). The stereom is openly labyrinthic over the inner and outer faces and towards the anterior process, but thickened at the edges. In some examples the internal face of the anterior process appears imperforate (Pl. 6, fig. 2). The stereom is denser on the frontal excavations (Pl. 6, fig. 8) and the side of the anterior process (Pl. 6, fig. 5).

Discussion. This type of calcareous ring is most similar to that of the Recent family Myriotrochidae (order Apodida). In myriotrochids the radials differ from the interradials by sometimes having a perforate anterior process, of which there is one possible example in the fossil material, and sometimes a double anterior process, of which there is at least one specimen from the Blue Lias (Pl. 6, fig. 10). In addition, a posterior process, as seen in BMNH E27422 (Pl. 6, fig. 9), is found only on radial elements, e.g. as in *Myriotrochus clarki* or *Siniotrochus myriodontus* (Gage and Billett 1986). Even considering this and further variation of Recent myriotrochids, such as the development of the posterior process in *M. clarki*, the gross morphology of the fossil examples is very variable and they may be derived from different myriotrochids. However, for the moment these elements are interpreted as all from one type of ring pending further material.

Amongst Recent myriotrochids two anterior processes occur only on the (dorso-lateral) radials of species which have twelve tentacles (Heding 1935). By inference the fossil species from which Type 2 elements are derived is assumed to have possessed twelve or more tentacles. Hess (1975) described similar myriotrochid elements of the calcareous ring from the Oxfordian of Switzerland.

Calcareous ring Type 3

One specimen, BMNH E27426, was recovered from sample H15 (Pl. 6, figs 3, 6). This has a very similar structure to that of the Type 2 elements, but has two discrete posterior processes which are not confluent with the lateral edges.

Discussion. The presence of posterior processes suggests that this is a radial element. It is most like the calcareous ring of the Myriotrochidae, by comparison with the Recent fauna and calcareous ring Type 2. It co-occurs in the same sample with several Type 2 elements, including BMNH 27422, of which it may be an aberrant form. However, there are no Recent myriotrochid radials with posterior processes like those seen here. Hence this element is tentatively separated from calcareous ring Type 2.

Calcareous ring Type 4

A single element, BMNH E27427, from a fourth type of ring was found in sample L42*b* (Pl. 6, fig. 7). Its stereom architecture indicates this is certainly echinoderm in origin. The symmetrical shape of the element, the presence of two apparent lateral faces, and a possible anterior process with a furrow on the internal (?) face and a notch at the end suggest that this is from a holothurian rather than any other echinoderm. Amongst holothurians this fourth type of element is most similar to the radials of some 'simple' types of ring found in the Dendrochirotida, e.g. the Cucumariidae, and the Dactylochirotida.

Relationship of calcareous ring and sclerites

The distribution of the four types of calcareous ring are compared with the more common sclerite components of the holothurian fauna (in Table 1). The percentage on the right indicates the probability of finding a particular morphotype when that type of ring is present in a sample. This is affected by the frequency with which each morphotype is found, i.e. the percentage is high for *Achistrum* because this morphotype is the most common throughout the succession. The left-hand column is more informative, giving an indication of the probability that a particular type of ring
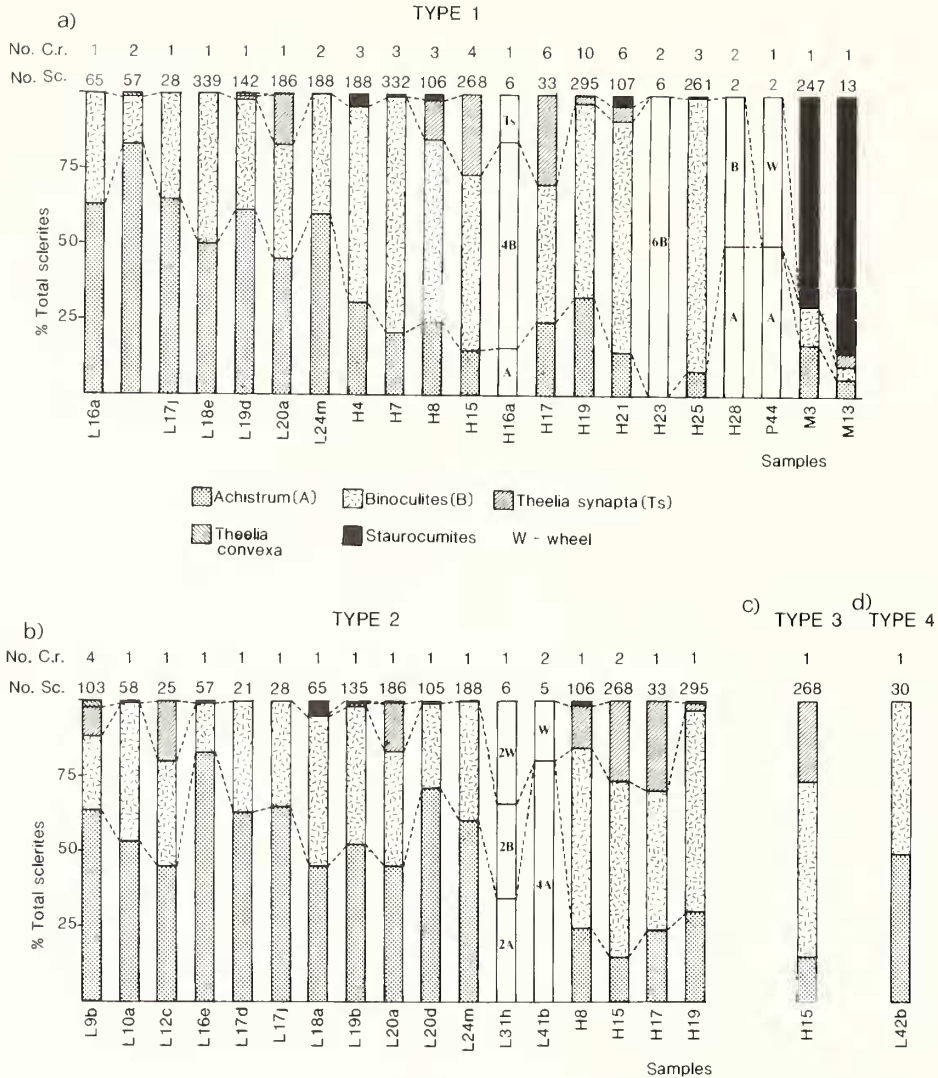
TEXT-FIG. 10. Number of elements of the calcareous ring (No. C.r.), total numbers of sclerites (No. Sc.) and the relative number of the main morphotypes for samples bearing: *a*, calcareous ring Type 1; *b*, Type 2; *c*, Type 3; *d*, Type 4.

will occur in a sample when a particular morphotype is also present. These percentages are more dependent on the relationship between the calcareous ring and sclerites than the frequency of the sclerites.

In Text-figure 10 the total number of elements of each type of ring is given together with the number of sclerites and the percentage composition of the sclerites. There is large variation in the number of sclerites relative to the number of elements of the calcareous ring (e.g. cf. *Staurocumites*, or total sclerites, with Type 1 in samples H19, M3 and M13), hence there is little point in trying to estimate the number of sclerites per individual of fossil species based on there being usually only 10–12 elements of the calcareous ring in most extant holothurians.

Calcareous ring Type 1 is derived from a molpadiid and probably the family Molpadiidae. In the

TABLE 1. The distribution of elements of the calcareous ring with respect to the most common sclerite morphotypes; bracketed figures are the number of samples in which both the calcareous ring and morphotype are found as a percentage of the total number of samples bearing that particular morphotype (on the left) or calcareous ring (on the right).

| Sclerite morphotype | Calcareous ring | | | | | | | |
| | Type 1 | | Type 2 | | Type 3 | | Type 4 | |
	No. samples	%	No. samples	%	No. samples	%	No. samples	%
Total	21	(25·0)	17	(20·5)	1	(1·2)	1	(1·2)
Achistrum	20 (95·2)	(26·0)	17 (100)	(22·1)	1 (100)	(1·3)	1 (100)	(1·3)
Binoculites/ Calclamna	20 (95·2)	(29·9)	16 (94·1)	(23·8)	1 (100)	(1·5)	1 (100)	(1·5)
Theelia synapta	8 (38·1)	(36·4)	8 (47·1)	(36·4)	1 (100)	(4·5)	—	—
Theelia convexa	3 (14·3)	(33·3)	5 (38·5)	(55·5)	—	—	—	—
Staurocumites	11 (52·4)	(55·0)	6 (35·3)	(30·0)	—	—	—	—

Blue Lias fauna the only possible molpadiid sclerite morphotype is *Staurocumites bartensteini*. The simplest interpretation, therefore, is that this morphotype and calcareous ring come from the same species. From Table 1 the most informative data, i.e. the left percentage column, support the association of Type 1 rings with *S. bartensteini*. However, it is surprising to find samples with Type 1 specimens but no *Staurocumites* (Text-fig. 10a).

Calcareous ring Type 2 is most closely comparable with that of the Myriotrochidae, but no distinctive myriotrochid wheels were recovered. However, the calcareous ring of hook-bearing body fossil material from the Carboniferous Francis Creek Shale is most similar to that of extant myriotrochids (personal observation) and hence the structure seen in the Myriotrochidae today may be primitive. Calcareous ring Type 2 is likely to be associated with one of the three apodan morphotypes found in the Blue Lias fauna, but as to which one it is difficult to conclude. *Achistrum* is far more abundant and frequent than either of the two apodan wheels, but the results in Table 1 indicate an association with *Theelia convexa*. A similar problem arises in establishing the sclerite morphotype associated with calcareous ring Type 3; the results in Table 1 favour an association with *Theelia synapta*. Alternatively, the Type 3 element may be an example of calcareous ring Type 2 indicating that this 'myriotrochid-like' calcareous ring was more variable than that of modern myriotrochids.

If the fourth type of ring element is dendrochirotacean in origin, then the most likely associated morphotype is *Binoculites*, interpreted to be from a dendrochirote, which is more common than other relevant morphospecies, e.g. *Palaeoypsilus*, and the only one to occur in the same sample.
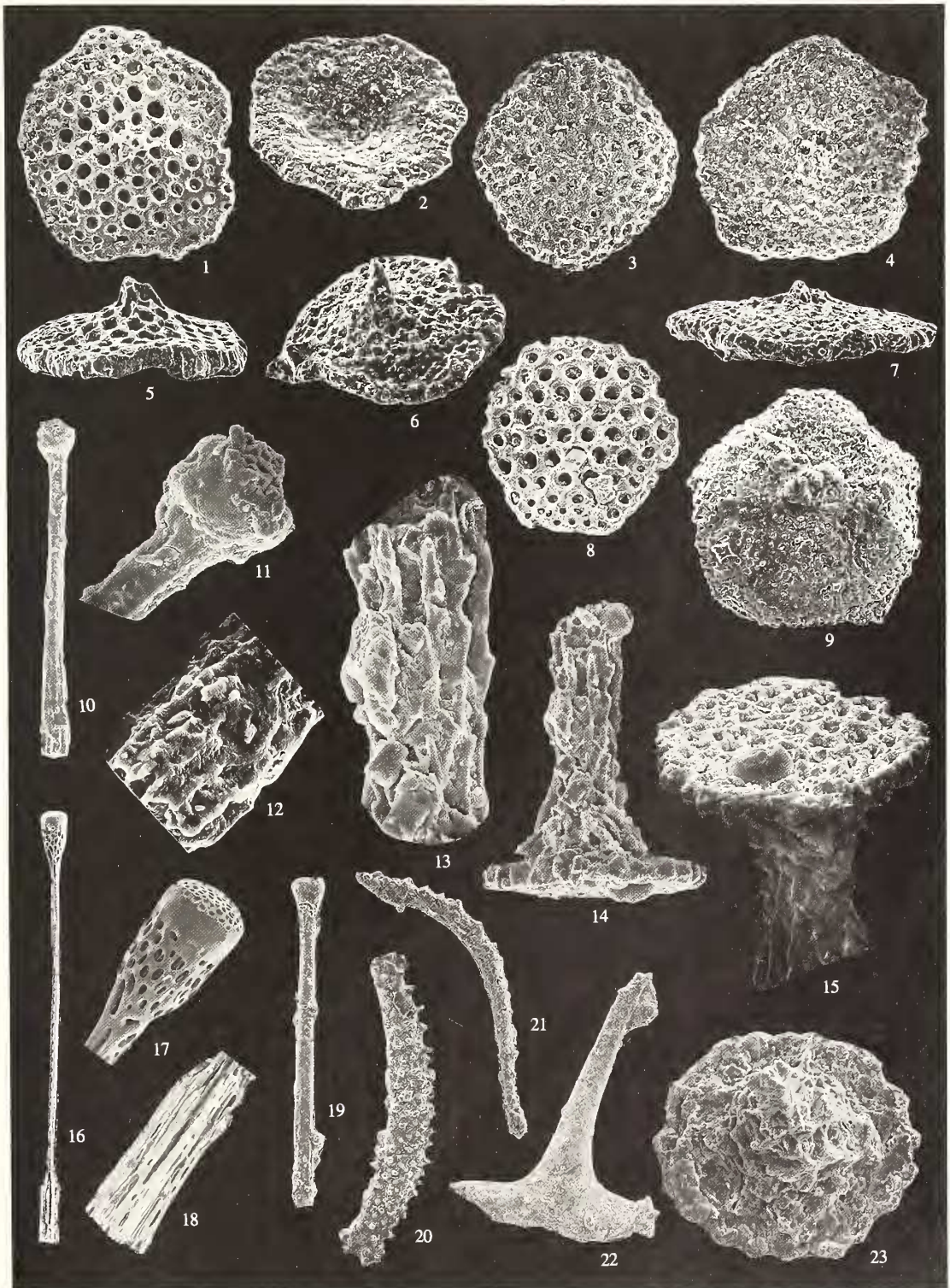
Even considering just the main sclerite taxa there appears to be one type of calcareous ring missing. Furthermore, Types 3 and 4 are each represented by a single specimen and calcareous ring structures are lacking in some samples with abundant sclerites. However, simple observations of Recent holothurians (Gilliland 1990) suggest that the ratio of sclerites to elements of the calcareous ring should be higher than even the most sclerite-laden samples from the Blue Lias. This could be because the relatively robust calcareous ring has a greater preservation potential, and/or post-mortem separation of an original calcareous ring/sclerite assemblage has occurred which is suggested by the variable distribution of the different calcareous ring types.

NON-HOLOTHURIAN 'HOLOTHURIAN SCLERITES'

The family Etheridgellidae. This family incorporates polygonal/subcircular, thickened, imperforate discs sometimes with a granular surface and a 'pseudospire'. Two genera were included in the Treatise, *Etheridgella* Croneis and *Frizzellus* Hampton (Frizzell and Exline 1966). A large number of such plates was recovered from all sections from the *planorbis* zone upwards. Previous authors have expressed doubts about whether these sclerites are from Holothuroidea. Frizzell and Exline (personal communication in Hampton 1958a) stated that plates from Recent ophiuroids were

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PLATE 2

GILLILAND, Blue Lias holothurian sclerites

'generically indistinguishable' from *Frizzellus*. Hampton (1958*a*) argued for their holothurian origin because of the close association of *Frizzellus* with other undoubted holothurian sclerites, and because it appeared to be closely related to *Etheridgella*. However, the association of *Frizzellus* with other sclerites indicates little and furthermore Pawson (personal communication in Lane 1976; Pawson 1980) did not think *Etheridgella* was a holothurian either. Lane himself presented a convincing case for a crinoid origin for some *Etheridgella*-type sclerites from the Pennsylvanian Lane Shale (Lane 1976). Frizzell and Exline (1966) included the complete Devonian fossil *Palaeocucumaria huusrueckiaua* in the Etheridgellidae on the basis of the body wall sclerites. As Lane correctly pointed out, no matrix-free ossicles of *Palaeocucumaria* have been examined and their preservation within the body wall, and published photographs, are not sufficient for a detailed description. It is probable that the original sclerites of this species have acted as the nuclei for the formation of pyrite blebs, hence destroying any morphological details.

Observations of *Etheridgella*-type plates from the Blue Lias indicate that the majority cannot be interpreted as holothurian. The plates are of variable shape, thickness and size, i.e. 160–360 μm. The edges of plates are often irregular implying that their growth had not ceased. Some specimens are opaque and brown in colour, a feature which Lane considered to be an important difference between *Etheridgella* and associated undoubted holothurian sclerites. However, in the Blue Lias examples the colour depends on the thickness of the plates and also varies in the accepted holothurian morphotypes. Sclerites of the *Etheridgella*-type occur together with a variety of other echinoderm material and sometimes in samples with no unequivocal holothurian sclerites, but there is no obvious relationship with any of the other echinoderm classes.

Within the *Etheridgella* material it is possible to distinguish a number of different forms: (a) flat to biconvex plates composed of a multilayered labyrinthic stereom with an average pore size of *c*. 15 μm (Pl. 1, fig. 18); these plates have a granular surface of small knobs; the ultrastructure, size and variation in the shape of these plates compare well with the disc scales of ophiuroids (Pl. 1, fig. 19); (b) squarish, multilayered plates with a smooth surface and more solid appearance compared with type (a) due to thickened trabeculae and occluded pores (Pl. 2, fig. 3); some specimens of *Frizzellus irregularis* are very similar (Pl. 2, fig. 9); (c) strongly concavo/convex, circular plates, imperforate on the concave side and with a stereom meshwork on the convex side (Pl. 2, figs 2, 6); a thin or thick prominent projection is developed from the centre of the stereom structure; plates of this kind are not known in holothurians; and (d) polygonal plates, slightly concave in the centre, with large (*c*. 10 μm) regularly arranged holes in the middle and smaller (*c*. 5 μm) holes towards the periphery (Pl. 2, figs 1, 5); a short projection or spire comprising several struts extends vertically from the central convex area; similar convex plates without a spire may be early growth stages (Pl. 2, fig. 8; a plate with a spire and a single layered stereom is more likely to be holothurian than non-holothurian in origin; however, examples occur which are intermediate in morphology with 'type (a)' plates (Pl. 2, figs 4, 7).

The morphology of (a)–(c) above precludes assigning them to holothurians. Hampton's original material of *Frizzellus irregularis* in the collections of the British Museum (Natural History) shows a similar wide morphological variation. The position of type (d) is uncertain and for the moment it is preferable to classify it as echinoderm in origin rather than specifically holothurian. Some taxa of the Etheridgellidae, at least, seem to be derived from crinoids and ophiuroids.

Rhabdotites-type rods. Frizzell and Exline (1955) recognized two species of the morphogenus *Rhabdotites* Deflandre-Rigaud which are simple, straight to slightly curved rods with a knob at each end. *Rhabdotites rectus* Frizzell and Exline, originally described from the Middle Triassic, is now accepted to be the roveacrinid (somphacrinid) microcrinoid *Osteocrinus rectus* (Kristan-Tollmann 1970).

Rods attributable to *Rhabdotites* were found in several samples from the Blue Lias. These rods are straight, long and thin, with a knob at one end and a slight increase in diameter at the other end (Pl. 2, figs 10, 19). The rods are not solid throughout but composed of stereom meshwork in parts. Over most of the shaft there are grooves which become deeper towards the knob (Pl. 2, fig. 11). The

knob itself is pitted producing a 'pepper-pot' sculpture which may be obscured if poorly preserved. At the opposite end a steorem of longitudinally arranged holes and grooves occurs all the way round.

The ultrastructure of the rods indicates clearly that they are not derived from holothurians or roveacrinids. They do, however, compare closely with stalks of echinoid pedicellaria (i.e. Pl. 2, figs 16–18). The Blue Lias includes a variety of echinoid debris derived from *Eodiadema* and *Diademopsis* and the *Rhabdotites*-type elements are considered to be pedicellarial stalks from one of these two genera.

Some previously described records of *Rhabdotites* are also probably derived from echinoids. Hampton (1957) referred a single specimen (BMNH E27042) from the Upper Bathonian to *Rhabdotites?rectus*. This specimen has a similar ultrastructure to the Blue Lias rods, though this has been largely obscured (Pl. 1, figs 21–22). Likewise, a badly preserved specimen of *R. rectus* with a knob at only one end, described by Zawidzka (1971), should not be accepted as holothurian in origin.

Curved spiny rods. Variably curved rods (Pl. 2, figs 20–21) occur throughout the section. These rods are spiny over much of the surface, or at least along the outer curve, though poor preservation may obscure this.

Curved spiny to smooth rods occur in some Recent holothurians, e.g. the Stichopodidae. However, similar spicules are found in several octocoral groups such as the Alcyonacea and Gorgonacea (e.g. see Bayer 1956; Deflandre-Rigaud 1957). Octocoral rods are more or less strongly sculptured by spines or 'warts', whereas holothurian rods are usually sculptured along one edge and not to the same extent. The Blue Lias examples are most probably octocoral in origin. Specimens in which there appear to be spines along one edge only cannot be accepted as holothurian because they intergrade with more spiny examples and because all the spines except those seen in profile may be obscured if poorly preserved.

Anchor-shaped sclerite. One anchor-shaped sclerite was recovered from sample L18a (Pl. 2, fig. 22). It is about 450 μm long and the shaft is thick, becoming wider and curving round to form two arms at one end. The other end is broken so it is not possible to determine if a 'stock' structure is present or not. Anchor-shaped sclerites occur in both holothurians and other groups, particularly sponges. Holothurian anchors differ from the Blue Lias specimen because the shaft is normally long and slender with the widest section in the middle, and there is a sharp angle between the shaft and the curved arms. The anchor sclerite is more similar to those previously assigned to sponges (see Mostler 1972d).

Eocaudina-type plates. Various echinoderm plates were found throughout the succession (Pl. 1, figs 10–11). Most comprise a single layer of retiform stereom whilst some also have a secondary layer. Holes may be regularly arranged (Pl. 1, fig. 11), or irregularly arranged and variable in size, e.g. 5–50 μm. Such plates are usually assigned to the holothurian morphogenus *Eocaudina*. However, as some authors have noted, *Eocaudina* cannot be considered unequivocally holothurian in origin since these plates are also found in other echinoderms (Frizzell and Exline 1955). In the Blue Lias *Eocaudina* co-occurs with both holothurian and other echinoderm skeletal elements. It seems preferable, therefore, not to accept these plates as holothurian.

SYSTEMATIC PALAEONTOLOGY

The systematic section is arranged, where possible, in terms of the Recent biological classification. Because of the artificial taxonomy normally employed for fossil holothurian sclerite classification the parafamily Priscopedatidae appears under several different Recent orders and hence, to avoid confusion, is placed in square brackets subsequent to its first appearance.

Class HOLOTHUROIDEA
Order DACTYLOCHIROTIDA Pawson and Fell, 1965
or DENDROCHIROTIDA Grube, 1840
(sometimes united in the sub-class DENDROCHIROTACEA Grube, 1840)
Parafamily PRISCOPEDATIDAE Frizzell and Exline, 1955 *pars*

Type species. Priscopedatus pyramidalis Schlumberger, 1890.

Diagnosis. Fossil sclerites in the form of tables or spired plates comprising a perforated base, or disc, and a spire and/or stirrup.

Discussion. In Frizzell and Exline (1966) the Priscopedatidae includes tables only, of which there are four genera as distinguished by Deflandre-Rigaud (1962). One of the main diagnostic characters used in their classification was the number of branches in the stirrup and/or spire, being either three (*Dictyothurites, Priscularites*) or four (*Priscopedatus, Staurocumites*). Soodan (1975) revised the classification, following the addition of *Priscolongatus* Gorka and Luszczewska, 1969, and recognized the new genera *Clarkina, Feddenella, Fletcherina, Hannaina,* and *Sastriella,* using the number of central holes and the shape of the base as differentiating characters. Spired plates were not included in either of these schemes because, in the case of the former, no fossil examples had been found and, in the latter case, because the only definite fossil spired plate had been incorrectly placed in the genus *Priscopedatus.* The parafamily Priscopedatidae is enlarged here to include spired plates. Tables occur in four of the six Recent orders of holothurians and the Priscopedatidae is therefore polyphyletic. Spired plates are found in several families of the order Dactylochirotida and one family of the Dendrochirotida, the Paracucumidae (Gilliland 1990). Those fossil examples that cannot be referred to one of these orders only are considered first, followed by any that can be.

The spired plates described below are distinct from any existing genus of table, having more than four pillars (tables usually have four or less) which become intertwined. Additionally the disc may have a reticulate network, composed of more than one calcareous layer, that cannot be easily differentiated from the base of the spire. Spired plates are not assigned to a separate parafamily because of their similarity to, and possible morphological intergradation with, certain tables (see Gilliland 1990, Section 2.3.4).

A comparison with Recent spired plates indicates that the differences between the fossil forms are as great as those between Recent genera and they should therefore be placed in more than one morphogenus.

Genus CLAVALLUS nov.

Etymology. From the Latin *clavallus,* club-like, in reference to the shape of the spire.

Type species. Priscopedatus spicaudina (Gutschick *et al.,* 1967).

Diagnosis. Plates with a spire that is noticeably expanded in the top third and is placed near to the

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EXPLANATION OF PLATE 3

Figs 1–2, 4–5. *Theelia convexa* (Whidborne). 1, E27239; L16*e*; *angulata* zone, ×215. 2, E27130; L9*b*; *laqueus?extranodosa/complanata* subzone, ×255. 4–5, E27240; L17*j*; *angulata* zone, ×240, ×1180, respectively; t = teeth.
Figs 3, 6. *Acutisclerus plagiacanthus* sp. nov. Holotype; E27349; L23*f*; *angulata* zone, both ×110.
Figs 7–15. *Theelia synapta* sp. nov. 7, Holotype; E27208; L9*b*; *laqueus?extranodosa/complanata* subzone, ×360. 8, Paratype; E27186; H13; *bucklandi* subzone, ×195. 9, 12, E27256; L20*a*; *angulata* zone, both ×185. 10, Paratype; E27312; L20*a*; *angulata* zone, ×230. 11, Paratype; E27159; H15, *bucklandi* subzone, ×130. 13, E27257; L20*a*; *angulata* zone, ×200. 14, E27183; H15; *bucklandi* subzone, ×200. 15, E27175; H15; *bucklandi* subzone, ×740.
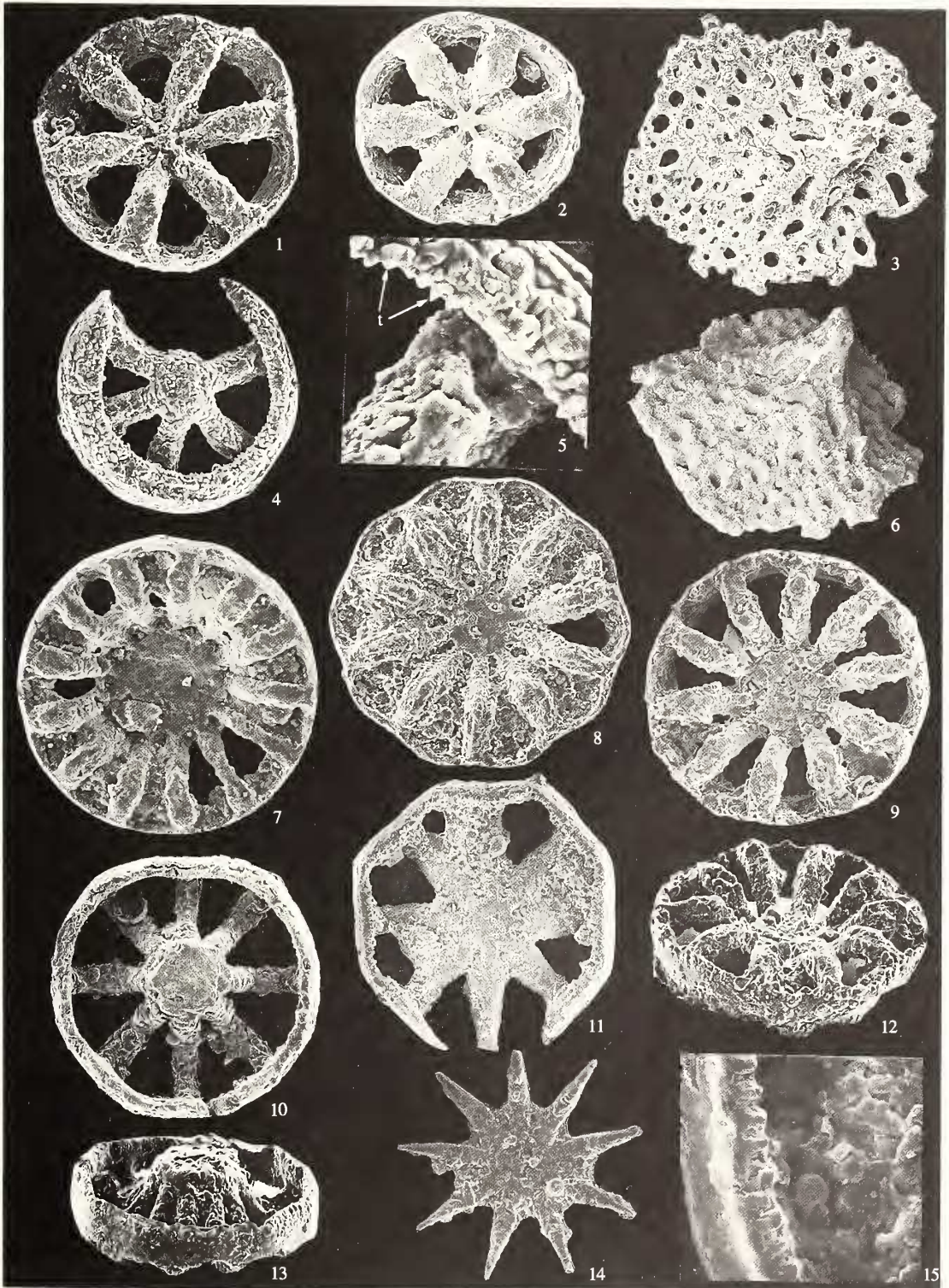
PLATE 3

GILLILAND, Blue Lias holothurian sclerites

centre of the plate. The base is composed of a single layer which curves slightly upwards into the base of the spire so that distinct pillars cannot be discerned. The spire is relatively tall compared to the plate diameter (height:diameter ratio > 0·6), smooth, and without obvious perforations over most of its area.

Remarks. This is a monospecific genus. The species is recorded from the Lower Carboniferous (Gutschick *et al.* 1967), the Upper Permian (*P.* cf. *spicaudina* Mostler and Rahimi-Yazd, 1976) and the Middle Triassic (*P.* cf. *spicaudina* Mostler, 1968*b*).

Genus ACUTISCLERUS nov.

Etymology. From the Latin *acutus*, pointed, in reference to the spire.

Type species. Priscopedatus empeldensis (Kristan-Tollmann, 1986).

Distribution. Lower Lias (Hettangian) of England, and Upper Lias (Pliensbachian) of Northern Germany.

Diagnosis. Round to oval plates with a spire comprising more than four pillars or struts which are bound together in an almost solid network and which converge to a point.

Remarks. Acutisclerus differs from Recent forms of spired plates in the way the spire converges to a point. The sculpturing of the spire and the morphology of the disc do not allow assignment to either the Dendrochirotida or Dactylochirotida.

Acutisclerus plagiacanthus sp. nov.

Plate 3, figs 3, 6

Etymology. From the Greek *plagio*, to the side, and *acanthus*, a thorn or spine, in reference to the leaning spire.

Types. Only one specimen, the holotype, BMNH E27349, from the *angulata* zone of Long Itchington.

Diagnosis. Irregularly bound, sub-oval plate perforated by irregularly distributed (i.e. not closely packed) circular to oval holes, with an eccentrically placed spire. The spire has a broad base formed from many (> 4) struts that coalesce and converge to a point. The spire is oblique, rather than perpendicular, to the base plate.

Dimensions. Length of plate, 460 μm; maximum width, 395 μm; spire height, 160 μm; hole diameter, 8–50 μm.

Description. A spired plate comprising a sub-oval base and a 'leaning' spire. The edge of the plate is irregular and probably still developing. The plate is perforated all over by variably sized and irregularly arranged holes, most of which are relatively small (< 30 μm) and separated by equally sized struts. The smallest holes are circular while larger holes are oval. The spire rises from the plate at about 60° at about one third along the length of the base plate. The spire is composed of 8 or more struts intermingled with the stereom of the base plate and extending over a wide area of about 170 μm in diameter. The struts coalesce to form a spire of much smaller diameter than its base.

Remarks. A. plagiacanthus differs from *A. empeldensis* in that the spire leans obliquely and the base of the spire occupies a relatively larger area.

Order DACTYLOCHIROTIDA Pawson and Fell, 1965
Family YPSILOTHURIIDAE Pawson and Fell, 1965

Diagnosis. Dactylochirotids with body wall formed of large plates each with a spiny spire.

Remarks. Although there are soft tissue characters which identify ypsilothuriids the structure of the spired sclerites is highly distinctive. In the Vaneyellidae the spire is relatively short.

[Parafamily PRISCOPEDATIDAE Frizzell and Exline, 1955] *pars*
Genus PALAEOYPSILUS nov.

Etymology. After the Recent holothurian family Ypsilothuriidae.

Type species. *Palaeoypsilus liassicus* sp. nov.

Diagnosis. Spired plates consisting of a circular, regularly perforated base, relatively small compared to the height of the spire, and a prominent spiny spire, widest at the bottom, comprising many vertical struts interlocking along the length of the spire.

Remarks. Amongst the spired plates of Recent taxa only those of the Ypsilothuriidae possess a tall, spiny spire. However, the base plate of *Palaeoypsilus* is both smaller than that of Recent ypsilothuriids and has a proportionally taller spire. Hence the specimens described below are assigned to a new genus rather than one of the three existing ypsilothuriid genera. However, *Palaeoypsilus* resembles other ypsilothuriid spired plates with respect to other characters and the irregular edge of the plate suggests that the plate may still be developing.

Palaeoypsilus liassicus sp. nov.
Plate 2, figs 13–15, 23

Etymology. After the Lias.

Types. Holotype, BMNH E27338 (Pl. 2, figs 13–15); paratypes, BMNH E27334 (Pl. 2, fig. 23), E27339; all from the *bucklandi* subzone of Hock Cliff.

Other material. One specimen from the *bucklandi* subzone of Hock Cliff and one from the *laqueus*? subzone of Long Itchington.

Diagnosis. A spired plate with a circular, regularly perforated base and a massive, long, thorny spire comprising many interlocking, vertical struts.

Dimensions. Diameter of base, 140–180 μm; spire height is greater than the diameter.

Description. Spired plates with a circular base plate and undulating periphery imparting a spiny appearance (Pl. 2, fig. 23). The base is perforated by small, round, regularly arranged and equal-sized holes. A large, robust spire rises centrally and is formed of many interlocking elongate vertical struts connected by crossbars (Pl. 2, fig. 13). The spire is widest at the bottom where additional struts have developed from the base plate. A thorny effect is produced from small outgrowths along the length of the struts (Pl. 2, fig. 13).

Remarks. Recent ypsilothuriid plates are much larger (usually 1 mm or more in diameter) than those of *Palaeoypsilus liassicus*. Recent examples also co-occur with unspired plates, of which there are possible examples in the Blue Lias fauna (see Etheridgellidae and *Eocaudina*-type plates above), and dendrochirotacean irregular rods (Gilliland 1990, Section 2.3.4) of which no examples were recovered. The lack of rods may, however, be due to the rarity of *P. liassicus*.

Order DENDROCHIROTIDA Grube, 1840
Parafamily CALCLAMNIDAE Frizzell and Exline, 1955 *pars*

Diagnosis. Flat to concavo-convex perforate plates, usually thin and rarely multilayered. Shape is

variable and commonly the edge appears to be incompletely formed, i.e. it is highly scalloped. The perforations are not denticulate and there is no socket, strap or spire.

Discussion. Calclamnidae includes a large number of genera some of which cannot be considered unequivocal holothurians, e.g. *Eocaudina*, *Mortensenites* or *Petropegia*. Thus the family may be polyphyletic by inclusion of sclerites from several different echinoderm classes. Pawson (1966) included all Calclamnidae within the order Dendrochirotida but, given the wide occurrence of plates in the Recent fauna, the family is probably also polyphyletic with respect to holothurians. Many of the genera may be assigned to the Dendrochirotida, including *Binoculites* (as defined here). However, *Calclamnella* (as defined here) includes sclerites found in the Aspidochirotida.

Genus BINOCULITES Deflandre-Rigaud, 1952 emend

Type species. Binoculites terquemi Deflandre-Rigaud, 1952.

Other species. B. jurassica (Frizzell and Exline, 1955).

Diagnosis. Perforate, elongate buttons or plates, usually bilaterally symmetrical, with one or more terminal holes at each end. Between the terminal holes there are either two rows of holes, one on each side of the midline, or just two holes producing a cruciform pattern together with the terminal holes. Early growth stages are dumb-bell-shaped rods in which only the terminal holes are present.

Remarks. The genus *Binoculites* was formerly restricted to the dumb-bell-shaped rods and included in the parafamily Stichopitidae. However, *Binoculites*, so defined, merely represents the early growth stages of plates of the genus *Calclamna* and should be placed in the family to which these plates are assigned, i.e. the Calclamnidae. Following ICZN regulations the generic name *Binoculites* is retained with *Calclamna* Frizzell and Exline, 1955 reduced to synonymy. The genus *Calclamnella* Frizzell and Exline, 1955 is retained for plates similar to *Binoculites*, as defined here, but in which no terminal holes are present. *Binoculites* may be assigned to the Recent order Dendrochirotida and closely resembles sclerites of, for example, some species of the family Cucumariidae.

Binoculites terquemi Deflandre-Rigaud, 1952 emend

Plate 1, figs 1–9, 20

1875   'Spicules de tube ambulacraire de radiaires' Terquem and Berthelin (*pars*), p. 109, pl. 9, fig. 9*a*.
1876   Crinoid arm segments? Blake, p. 448, pl. 17, fig. 45.
1908   *Uncinulina polymorpha* Terquem (*pars*); Issler, pp. 95–97, pl. 7, figs 346–350, 352–353, 358–360 (not figs 351, 354–357, or 361–362).
1932   *Uncinulina polymorpha* Terquem (*pars*); Croneis and McCormack, p. 128, pl. 18, figs. 48–49, 56, 60–63, 65 (not figs 53, 64 or 66–68).
1935   ?Holothuroidea Henderson, pp. 555–556, text-fig. 3*m*.
1936   Anker-Platten Bartenstein, pp. 2–4, text-figs 2*a–b*, 7 (excluding lower left specimen).
1937   'Spicules of holothurians' Mortensen, pp. 25–26, pl. 4, figs 8–9, 16–19.
1937   Holothurien-Ankerplatten Bartenstein and Brand, p. 439, pl. 2A, fig. 24.
1950   'Nadel (Spicula) einer dendrochiroten Holothurie' Schindewolf, text-fig. 89.
1952   *Binoculites terquemi* Deflandre-Rigaud, p. 6.
1953   *Binoculites terquemi* Deflandre-Rigaud; Deflandre-Rigaud, p. 953, text-fig. 11.
1955   *Binoculites irregularis* Frizzell and Exline, p. 67, pl. 1, figs 16–17.
1955   *Binoculites issleri* Deflandre-Rigaud (*pars*); Frizzell and Exline, p. 68, pl. 1, figs 19–21 (not fig. 18).
1955   *Binoculites terquemi* Deflandre-Rigaud; Frizzell and Exline, p. 69, pl. 1, figs 24–26.
1955   *Calclamna germanica* Frizzell and Exline, pp. 76–77, pl. 2, figs 1–5.
1955   *Calclamnoidea irregularis* Frizzell and Exline, p. 82, pl. 2, fig. 18.
1961   *Binoculites issleri* Deflandre-Rigaud; Rioult pp. 130–131, table 1, fig. 8.
1961   *Binoculites irregularis* Frizzell and Exlinc, forms β and γ Rioult, p. 130, table 1, figs 7, 16.

1961   *Binoculites* cf. *irregularis* Frizzell and Exline, Rioult, p. 130, table 1, fig. 3.
1961   *Binoculites terquemi* Deflandre-Rigaud, form β Rioult, p. 129, table 1, fig. 5.
1961   *Calclamna germanica* Frizzell and Exline, forms α and β Rioult, pp. 132–133, table 1, figs 4, 9.
1966   *Binoculites issleri* Deflandre-Rigaud (*pars*); Frizzell and Exline, p. U662, text-fig. 529 (3c) (not 3b).
1966   *Binoculites terquemi* Deflandre-Rigaud; Frizzell and Exline, p. U662, text fig. 529 (3a).
1966   *Calclamna germanica* Frizzell and Exline; Frizzell and Exline, p. U664, text-fig. 530 (1a–b).
1968   *Calclamna* cf. *germanica* Frizzell and Exline; Speekmann, pp. 199–200, pl. 1, fig. 5.
1972   *Binoculites irregularis* Frizzell and Exline; Miehelson, p. 61, pl. 2, figs 2–3.
1973   *Calclamna germanica* Frizzell and Exline; Michelson, pp. 61–64, pl. 1, figs 1–18; pl. 2, figs 4–8; pl. 3, figs 1–6.
1978   *Binoculites irregularis* Frizzell and Exline form β Rioult?; Copestake, pl. 32, fig. 7.
1986   *Binoculites issleri* Deflandre-Rigaud; Kristan-Tollmann, p. 130, pl. 29, fig. 1.

Types. The leetotype (seleeted by Frizzell and Exline 1955, pl. 1, fig. 24) was originally described by Mortensen 1937 (pl. 4, fig. 8). Mortensen described one other specimen in the syntype series (pl. 4, fig. 9).

Material studied. Over 1500 specimens including BMNH E27267–27272, E27279, E27295–27296, E27301, E27313–27316, E27320–27330, E27344. The material comes from Hock Cliff (*bucklandi* subzone), Long Itchington (?*portlocki–reynesi* subzones), Maisemore Cliff (*rotiforme* subzone) and Pinhay Bay (*portlocki–laqueus, rotiforme–sauzeanum* subzones).

Stratigraphic range. Middle Triassic (Anisian) to Lower Jurassic (Upper Pliensbachian).

Diagnosis. A species of *Binoculites* which is relatively short and wide. There are usually two prominent holes at either end of the long axis and two larger holes in the central area either side of the mid-line. Additional holes, usually about half the size of the first formed terminal holes, occur at either end.

Dimensions. Fully developed examples vary in length from 150 to 500 μm and in width from 150 to 310 μm. The widest part is normally towards the middle and the width between 50 and 90 % of the length. In the earliest growth stage the widest part of the sclerite is at either end and is 20–30 % of the length. A few early growth stages were found which are larger (i.e. up to 750 μm in length) than any of the fully developed plates (Pl. 1, fig. 3).

Description. The earliest growth stages are relatively short and wide at the expanded ends (Text-fig. 7) with a large hole in the expanded part. Growth outwards from the expanded ends results in the addition of holes which are still quite large but usually smaller than the first formed hole (Pl. 1, fig. 2). Further aeeretion proeeeds towards the middle from the two ends eventually joining up to form eentral holes whieh may be larger than or equal in size to the primary terminal holes (Pl. 1, figs 4, 9). Very small holes may oeeur around the periphery (Pl. 1, fig. 4). The relative length/width of the plates varies from long and thin to short, wide button-like forms. The orientation of the central holes also varies. Oeeasionally a bar grows aeross one of the eentral holes dividing it in two (Pl. 1, fig. 5).

Discussion. *B. terquemi* is a well-defined species with different growth stages (= previously recognized morphotypes) which can usually be distinguished at all stages of growth from the closely related species *B. jurassica* (see Text-fig. 7 and discussion of the morphogenera *Binoculites* and *Calclamna* above). These differences include the size of the secondary holes at either end, which are quite large in *B. terquemi*, and the number of small holes around the entire periphery, of which there are very few in *B. terquemi*.

Binoculites jurassica (Frizzell and Exline, 1955) emend

Plate 1, figs 8, 12–17

1875   'Spieules de tube ambulacraire de radiaires' Terquem and Berthelin (*pars*), p. 109, pl. 9, fig. 9a.
1908   *Uncinulina polymorpha* Terquem (*pars*); Issler, pp. 95–97, pl. 7, figs 351, 354–357 (not figs 346–350, 352–353, 358–362).

1932   *Uncinulina polymorpha* Terquem (*pars*); Croneis and McCormack, p. 128, pl. 18, figs 64, 66–68
        (not figs 48–49, 56, 60–63, 65).
1952   *Binoculites terquemi* Deflandre-Rigaud (*pars*), p. 6.
1955   *Binoculites issleri* Deflandre-Rigaud (*pars*); Frizzell and Exline, p. 68, pl. 1, fig. 18 (not figs
        19–21).
1955   *Calclamnella jurassica* Frizzell and Exline, pp. 78–79, pl. 2, figs 11–13.
1961   *Binoculites terquemi* Deflandre-Rigaud, form γ Rioult, p. 130, table 1, fig. 14.
1961   *Calclamnella jurassica* Frizzell and Exline; Rioult, p. 133, table 1, fig. 13.
1966   *Binoculites issleri* Deflandre-Rigaud (*pars*); Frizzell and Exline, p. U662, text-fig. 529 (3*b*) (not
        3*c*).
1978   *Binoculites issleri* Deflandre-Rigaud; Copestake, pl. 32, fig. 4.

Types. The holotype of *Calclamnella jurassica*, as figured by Frizzell and Exline (1955; pl. 2, fig. 11), appears
not very representative of the species. However, this figure is a poor reproduction of the original plate given
in Issler 1908 (pl. 7, fig. 355) which shows the specimen to be characteristic of the species as defined here. The
holotype comes from the Upper Sinemurian of Ofterdingen, Schwabia, Germany. The paratypes proposed by
Frizzell and Exline include further specimens figured by Issler (pl. 7, figs 354, 356) which come from the Lower
Hettangian of Nurtingen, Schwabia. All of this material is located in the Geological Institute of Tübingen.

Material studied. Over 750 specimens including BMNH E27271, E27273–27274, E27277, E27280–27282,
E27285–27294, E27297–27300, E27303–27311 and E27317–27319. The material comes from Hock Cliff
(*bucklandi* subzone), Long Itchington (?*portlocki–conybeari* subzones), Maisemore Cliff (*rotiforme* subzone)
and Pinhay Bay (*portlocki–conybeari* subzones).

Stratigraphic range. Upper Triassic (Carnian) to Lower Jurassic (Upper Pliensbachian).

Diagnosis. A species of *Binoculites* which is relatively long and thin. Fully developed specimens have
two rows of usually larger holes either side of the mid-axis. In the earliest growth stages the two ends
of the rod are very narrow with a single small hole at the mid-axis. Smaller holes occur at the ends
of the sclerite and sometimes around the entire periphery.

Dimensions. Fully developed examples vary in length from 380 to 620 μm and in width from 190 to 300 μm.
The maximum width is central and varies between 40 and 50 % of the length. In the earliest growth stage the
widest part is at either end and varies between 10 and 25 % of the length. A few early growth stages were found
which are smaller, i.e. 195 μm in length, than any of the later growth stages.

Description. The earliest growth stage is relatively long and thin (Text-fig. 7) with a small hole occupying either
end (Pl. 1, fig. 13). Further development proceeds as for *B. terquemi*, but results in two rows of holes or,
perhaps more accurately, rows with more than one hole per row. The holes in the main (central) area of the

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EXPLANATION OF PLATE 4

Figs 1–8. *Achistrum monochordata* Hodson, Harris and Lawson. 1, E27137; L19*b*; *angulata* zone, × 80.
    2, E27140; H7; *bucklandi* subzone, × 300. 3, E27207; H13; *bucklandi* subzone, × 150. 4, E27123; P50;
    scipionianum subzone, × 125. 5, E27121; P26; *laqueus* subzone, × 115. 6, E27136; L19*d*; *angulata* zone,
    × 115. 7, E27128; L17*j*; *angulata* zone, × 120. 8, E27120; P26; *laqueus* subzone, × 140.
Figs 9–16, 21. *Staurocumites bartensteini* Deflandre-Rigaud. 9, E27224; M13; *rotiforme* subzone, × 235.
    10, E27210; M3; *rotiforme* subzone, × 380. 11, E27266; M3; *rotiforme* subzone, × 225. 12–13, E27221; M3;
    rotiforme subzone, both × 385. 14, E27203; M3; *rotiforme* subzone, × 230. 15, E27265; M3; *rotiforme*
    subzone, × 240. 16, E27204; M3; *rotiforme* subzone, × 230. 21, E27211; M3; *rotiforme* subzone, × 230.
Figs 17, 19–20, 22. *Praeeuphronides multiperforata* Mostler. 17, E27353; L23*f*; *angulata* zone, × 75. 19, 22,
    E27352; L23*f*, *angulata* zone, × 195, × 230, respectively. 20, E27354; L23*f*; *angulata* zone, × 155.
Figs 18, 24. *Priscopedatus* sp. nov.? Holotype; E27342; L9*b*; *laqueus?extranodosa/complanata* subzone,
    × 585, × 600, respectively.
Fig. 23. *Punctatites*? aff. *extensus* (Mostler). E27222; L18*e*; *angulata* zone, × 75.
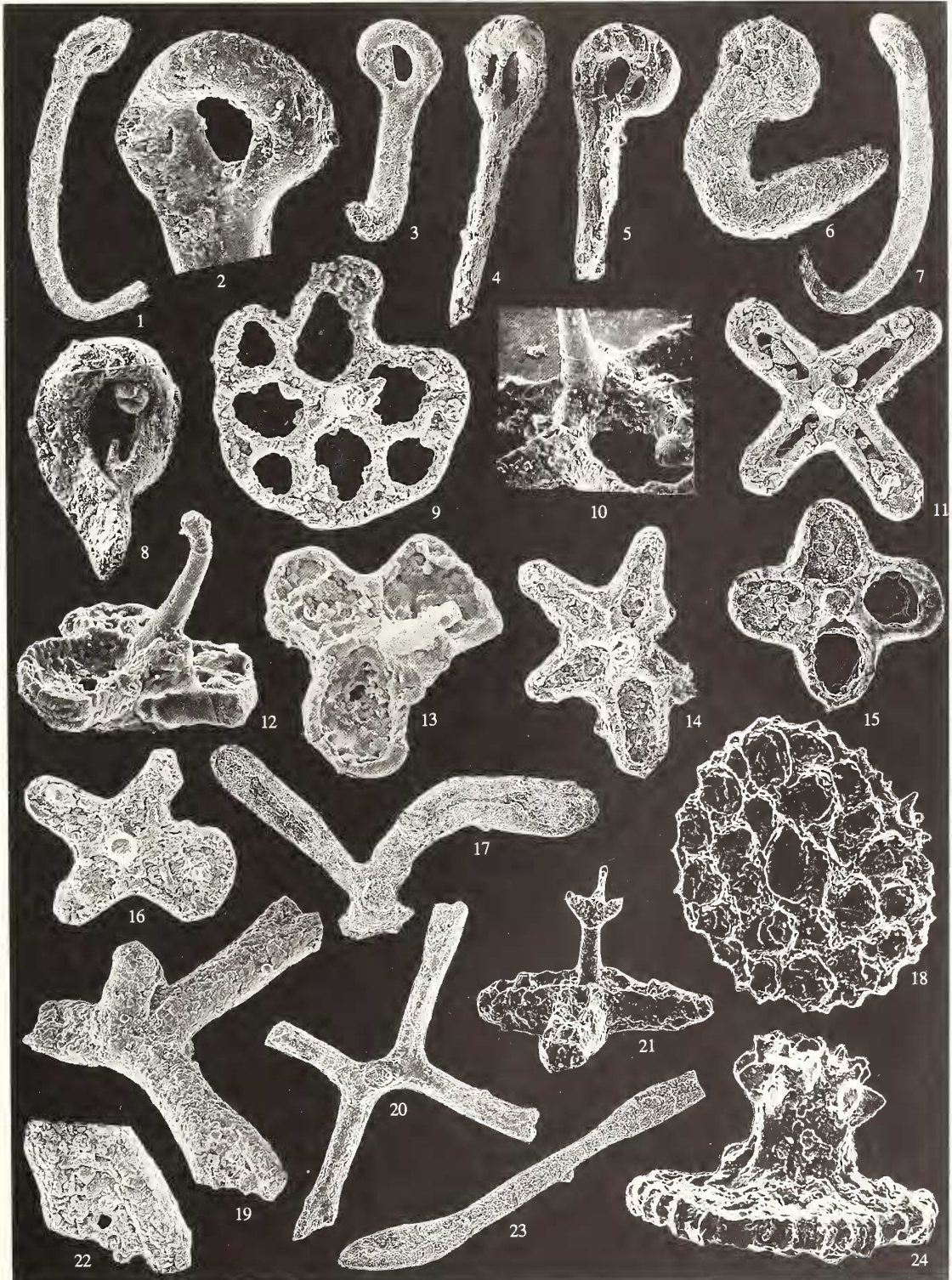
PLATE 4

GILLILAND, Blue Lias holothurian sclerites

fully developed plate are larger than the terminally placed holes. As in *B. terquemi* the orientation of the central holes varies. The additional 'secondary' holes at the two ends tend to be very small and may continue around the entire periphery.

Discussion. Although *Binoculites issleri* precedes *Calclamnella jurassica* by three years the trivial name used here is *jurassica*. This is because *B. issleri* was originally defined on material referable to both *B. jurassica* and *B. terquemi* (as defined here) and the holotype is a form assignable to *B. terquemi* (see Frizzell and Exline 1955, pl. 1, fig. 20). Thus, *B. issleri* is a junior synonym of *B. terquemi*. The oldest available name for the material described here is therefore *Calclamnella jurassica*, although the generic name is subordinate to *Binoculites*. *B. jurassica* and *B. terquemi* differ in several ways as discussed above.

Order ELASIPODA Théel, 1882
Parafamily STICHOPITIDAE Frizzell and Exline, 1955 *pars*
Genus PRAEEUPHRONIDES Mostler, 1968*b*

Type species. *Praeeuphronides multiperforata* Mostler, 1968.

Other species. The genus includes seven other species: *P. concavus* Mostler, 1972*b*; *P. complexus* Kozur and Mock, 1972; *P. crassiramosus* Mostler, 1972*a*; *P. latus* Mostler, 1972*b*; *P. robustus* Mostler, 1970; *P. simplex* Mostler, 1969; and *Praeeuphronides* n. sp. Kozur and Mock, 1972.

Stratigraphical age and distribution. Middle Triassic (Upper Anisian) to Lower Jurassic (Middle Lias) of Austria, Czechoslovakia, Rumania, and the Indian Himalayas.

Diagnosis. Sclerites comprising a rod with four arms in one plane. The distal part of each arm is expanded and bears numerous small holes usually lying within a groove. A large spine or apophysis, with variably developed sculpturing, usually occurs in the centre of the rod.

Remarks. *Praeeuphronides* exhibits a wide morphological variation and can be compared with several Recent morphotypes. Mostler (1969) referred *Praeeuphronides* to the order Elasipoda deriving the name from the elasipod genus *Euphronides* (now *Psychropotes*). Hansen (1975) considered the resemblance to elasipod sclerites superficial and suggested a closer affinity with the Synallactidae (order Aspidochirotida). *Praeeuphronides* resembles synallactid sclerites more, both having four arms in one plane, the arms being perforated and expanded distally, and a single large, central spine. However, there is also gradation between *Praeeuphronides* and the fossil morphospecies *Palelpidia* which is accepted by both Hansen (1975) and Mostler (1969) to be elasipod. For the present, the latter evidence is more compelling and *Praeeuphronides* is referred to the Elasipoda (see Gilliland 1990, Section 5.10.2). The presence of holes within a groove at the end of the arms seems to be restricted to *Praeeuphronides*.

Praeeuphronides multiperforata Mostler 1968*b*

Plate 4, figs 17, 19–20, 22.

1968*a*   *Praeeuphronides multiperforata* Mostler, pp. 8–9, pl. 1, figs 2–3.
1968*b*   *Praeeuphronides multiperforata* Mostler; Mostler, pp. 430–431, text-fig. 1.
1968*c*   *Praeeuphronides multiperforata* Mostler, pl. 1, figs 9, 13.
1972   *Praeeuphronides* cf. *multiperforata* Mostler; Kozur and Mock, p. 11, pl. 5, fig. 2.
1972*a*   *Praeeuphronides multiperforata* Mostler; Mostler, p. 4 (listed only).
1973   *Praeeuphronides multiperforata* Mostler; Kozur and Mostler, p. 307 (listed only).
1973   *Praeeuphronides multiperforata* Mostler; Mostler and Parwin, pp. 12, 20, 30 (listed only).
1974   *Praeeuphronides* cf. *multiperforata* Mostler; Kozur and Mock, pl. 5, fig. 1.
1979   *Praeeuphronides multiperforata* Mostler; Mostler, p. 336 (listed only).

1980 *Praeeuphronides multiperforata* Mostler; Donofrio *et al.*, p. 68 (listed only).
1986 *Praeeuphronides multiperforata* Mostler; Soodan, pp. 64–65, pl. 1, fig. 1.

Types. Mostler (1968*a*) based his description on 36 examples from the Anisian 'Schreyeralm, obere Ammonitenlage' from Schreyeralm, Northern Austria, of which one, the holotype, was figured. All the material belongs to the Institut für Geologie und Paläontologie, Innsbruck.

Material. Five specimens (BMNH E27350–27355) from Long Itchington, sample L23*f* (*angulata* zone).

Stratigraphic range. Middle Triassic (Anisian) to Lower Jurassic (Upper Hettangian; Upper Sinemurian?).

Diagnosis. Praeeuphronides with four large divergent arms. The arms may be of unequal length but are all expanded distally. There is a well-developed groove in the expanded part with two or more rows of fine holes. The central spine is thick, varies in height relative to the length of the arms, and is expanded towards the top with small spines.

Dimensions. Maximum arm length, 239–420 μm; maximum arm width, 90–120 μm; spine height *c.* 90 μm.

Description. Flat sclerite comprising a short rod with four diverging arms. The arms are either straight (Pl. 4, fig. 20) or curved (Pl. 4, fig. 17), with arm width increasing distally. Along the expanded part is a groove perforated by two or more rows of small holes (Pl. 4, fig. 22). In the centre of the rod is a massive, circular, solid spine or apophysis which appears to be unsculptured (Pl. 4, fig. 19).

Discussion. Mostler (1968*b*) has discussed the large variability found in *Praeeuphronides multiperforata*. The variation seen in the present specimens is not significant. Although all the specimens come from one sample there appears to be nothing unique about the lithology or associated microfauna.

Order APODIDA Brandt, 1835
Parafamily THEELIIDAE Frizzell and Exline, 1955 emend Frizzell and Exline, 1966

Diagnosis. Concavo-convex wheels with spokes, separated by interspoke spaces, connecting a nonquadripartite central portion and an outer rim.

Remarks. Theeliidae includes wheels found in the apodan families Chiridotidae and Myriotrochidae and the larval wheels of the apodan family Synaptidae plus genera, such as *Micradites*, with unestablished affinities.

Genus THEELIA Schlumberger, 1890 emend

Type species. Chiridota undulata Schlumberger, 1890.

Diagnosis. Rim inclined to the plane of the wheel, curving upward and inward, and possessing regularly spaced teeth which do not extend to the periphery. The centre is imperforate, typically with a hemispherical or conical button or tubercle. Spoke number is variable, even within the same species, but is commonly less than ten.

Remarks. In their emended diagnosis Frizzell and Exline (1966) include spoke number as 6–10 but there are species, e.g. *T. convexa* with more than 10 (Lord and Senior 1973) and *T. variabilis* with less than 10 (Zankl 1966), which clearly indicate that this no longer holds.
    Two types of wheel-shaped sclerite are present in the Blue Lias. Both occur together in only 5 out of 26 samples and the distribution of the two species is not correlated.
    Maximum diameter, spoke number and number of teeth were recorded in order to determine if they were taxonomically diagnostic characters. There were few specimens with teeth visible over the
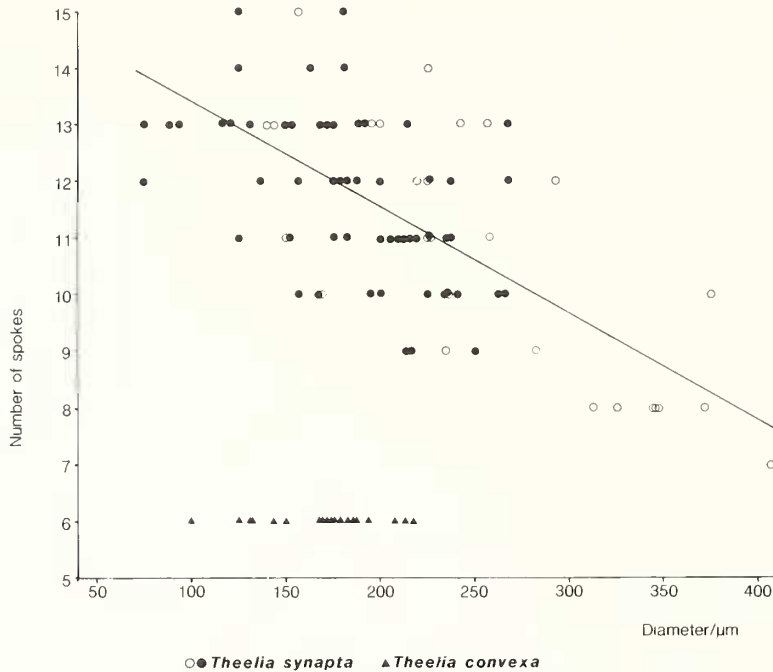
TEXT-FIG. 11. A plot of the number of spokes against wheel diameter of *T. synapta* ($n = 82$) and *T. convexa* ($n = 11$). The regression equation for *T. synapta* is: number of spokes = $15\cdot3-0\cdot0186$ diameter; R^2 value = $48\cdot1\%$, correlation coefficient = $-0\cdot698$ (cf. tabulated value of $0\cdot283$, at $P = 0\cdot01$). Open circles for *T. synapta* indicate data points from one sample (H15).

entire circumference so the number of teeth per quarter of the circumference was counted since they are regularly spaced around the inner edge. The relationship between diameter and number of spokes (Text-fig. 11) proved to be taxonomically useful, but that between diameter and number of teeth is not so informative (Text-fig. 12).

Family CHIRIDOTIDAE Östergren, 1907

Theelia convexa (Whidborne, 1883)

Plate 3, figs 1–2, 4–5

1883   *Chiridota convexa* Whidborne, p. 537, pl. 19, fig. 14, 14a.
1894   *Chiridota convexa* Woodward, p. 590 (check list only).
1917   *Chiridota convexa* Whidborne; Upton, p. 115.
1935   *Chiridota convexa* Whidborne; Fahrion, p. 12.
1936   *Chiridota convexa* Whidborne; Bartenstein, pp. 7–8.
1936   *Chiridota heptalampra* Bartenstein, pp. 6–8, text-figs 10a–b, 11a–b.
1951   *Chiridotites convexus* Whidborne; Deflandre-Rigaud, pp. 26–27, text-figs 47–48.
1951   *Chiridotites heptalampra* Bartenstein; Deflandre-Rigaud, pp. 27–28, text-figs 49–50.
1952   *Chiridotites heptalampra* Bartenstein; Deflandre-Rigaud, p. 9.
1955   *Theelia convexa* Whidborne; Frizzell and Exline, pp. 116–117, pl. 6, fig. 13.
1955   *Theelia heptalampra* Bartenstein; Frizzell and Exline, pp. 120–121, pl. 7, fig 1.
1961   *Chiridotites heptalampra* Bartenstein; Rioult, pp. 142–143, pl. 1, fig. 21.
1964   *Chiridota heptalampra* Bartenstein; Frentzen, p. 43, pl. 4, figs 18–21.
1965   *Theelia heptalampra* Bartenstein; Kristan-Tollman, p. 18.
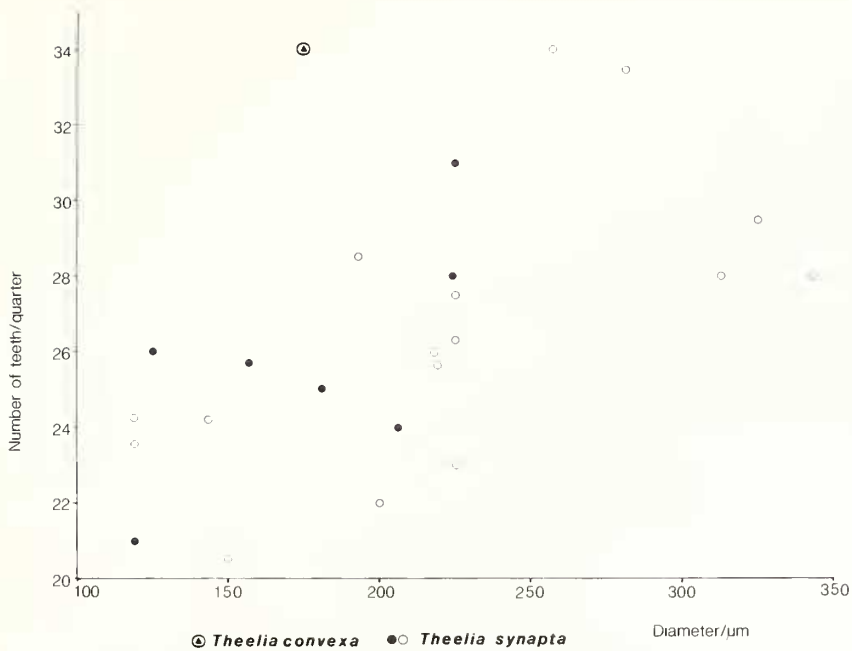
TEXT-FIG. 12. A plot of the number of teeth per quarter wheel circumference against wheel diameter in *T. synapta* (circles; $n = 23$) and *T. convexa* (triangle; $n = 1$). Open circles for *T. synapta* indicate data points from one sample (H15). Correlation coefficient for *T. synapta* is 0·631 (cf. tabulated value of 0·537, at $P = 0·01$).

1969	*Theelia heptalampra* Bartenstein; Garbowska and Wierzbowski, pp. 533–534, pl. 1, fig. 1; text-fig. 6 A–C.
1969	*Theelia heptalampra* Bartenstein; Gorka and Luszczcewska, p. 379, pl. 78, figs 1–3.
1972	*Theelia heptalampra* Bartenstein; Matyja, p. 240, text-fig. 8.
1972	*Theelia heptalampra* Bartenstein; Kozur and Mock, p. 22, pl. 11, figs 3–4.
1973	*Theelia convexa* Whidborne; Lord and Senior, pp. 36–37, pl. 1, figs 1*a*–*b*, 3*a*–*c*, 4*a*–*f*.
1975	*Theelia* cf. *heptalampra* Bartenstein; Hess, pl. 46, fig. 4.
1974	*Theelia heptalampra* Bartenstein; Kozur and Mock, pl. 7, fig. 6.

Types. Holotype, Sedgwick Museum J3741, from the Inferior Oolite, Bajocian (Middle Jurassic) of Burton Bradstock, Dorset.

Material studied. More than 20 specimens (including BMNH E27130–27131, E27193–27195, E27239–27240, E27243 and E27258–27259). The material comes from Pinhay Bay (*laqueus* and *conybeari* subzones) and Long Itchington (*laqueus, extranodosa/complanata* and *bucklandi* subzones).

Stratigraphic range. Upper Triassic (Upper Norian) to Upper Jurassic (Upper Oxfordian).

Diagnosis. Wheel with 6–11 strongly arched spokes. The hub lies within the plane of the rim which is strongly inclined to the plane of the wheel and is finely denticulate along the inner margin. On the ventral side there is a so-called 'star' formed of thin extensions of the spokes joined together above the hub.

Dimensions. Maximum diameter, 100–219 μm.

Description. Small wheels with a circular periphery and inner rim (Pl. 3, figs 2, 4). The latter is deep, strongly curved over (Pl. 3, fig. 2), and denticulate (Pl. 3, figs 4–5) with many small teeth although these may be difficult

to see due to poor preservation. Six spokes are consistently present (Text-fig. 11) although one badly preserved specimen may have seven spokes (diameter 175 μm). The spokes are relatively thick and either straight or widest in the middle (Pl. 3, figs 1–2). On the ventral side is a so-called 'star' comprising thin extensions of the spokes joined together and positioned in a flat plane above the hub. The main part of the hub is dome-shaped and concave below the star. The hub lies below (or within) the plane of the rim on both sides.

Discussion. The holotype is poorly preserved and in the original description Whidborne (1883) makes no mention of the 'star', and states that the inner rim is smooth. However, Lord and Senior (1973) included a photograph of the holotype, taken with a light microscope, in which both teeth and a star can be seen. The wheels described here are identical to Lower Bathonian material described in Lord and Senior (1973). Frizzell and Exline (1955, pl. 6, fig. 13b) incorrectly showed a low central boss on the ventral side of *T. convexa*.

Theelia heptalampra (Bartenstein, 1936), common in the Jurassic, is identical to *T. convexa* except in having 7, not 6, spokes. In some types of wheels such a small difference in spoke number is insignificant. However, in modern chiridotids it is rare to find wheels with other than 6 spokes. The sample size of the present material is small but there may be one specimen with 7 spokes. Further, Lord and Senior (1973) record *T. convexa* from the Lower Bathonian with 6–11 spokes (6 being the most common). *T. convexa* and *T. heptalampra* are therefore synonymized with *T. convexa* taking priority. *T. mortenseni* Deflandre-Rigaud (*non* Mortensen 1937, pl. 10, fig. 10) is similar to *T. convexa* but possesses larger (and fewer) teeth which is an important character (Rioult 1961) and distinguishes the two species. Other Jurassic wheels differ significantly in one or a few characters. *T. crassidentata* Deflandre-Rigaud has flat spokes and less numerous and larger teeth, *T. florida* Frizzell and Exline and *T. wartensis* Garbowska and Wierzbowski have a median ridge along the whole length of each spoke, and *T. dentata* Gorka and Luszczewska possesses an undulating periphery, different spoke structure and an irregularly developed star i.e. the 'arms' of the star may not necessarily correspond to the centre of the spoke and there is not an extension from every spoke. An irregular star is also characteristic of *T. stellifera* Zankl, an Upper Triassic morphospecies with a wide variation. Kozur and Mock (1972) suggested that the 6-spoked subspecies *T. stellifera bistellata* may be synonymous with *T. heptalampra*, but the consistently irregular 3-armed star of the former distinguishes them. In *T. terquemi* Deflandre-Rigaud the undulating periphery and spokes, which are very wide in the middle, distinguish it from *T. convexa*.

T. convexa is undoubtedly a member of the Recent family Chiridotidae, but is unusual in the large variation in spoke number that it displays.

Family SYNAPTIDAE Burmeister, 1837

Theelia synapta sp. nov.

Plate 3, figs 7–15

Etymology. After the resemblance to the wheels found in the larvae of the Recent family Synaptidae.

Types. Holotype, BMNH E27208, from the *liasicus* zone of Long Itchington (Pl. 3, fig. 7); paratypes, BMNH E27159, E27186 from the *bucklandi* zone of Hock Cliff (Pl. 3, figs 8, 11) and BMNH E27312 from the *angulata* zone of Long Itchington (Pl. 3, fig. 10).

Other material. Over 130 specimens, including BMNH E27141–27192, E27208, E27228, E27230–27238, E27241–27242, E27244–27257, and E27312, only some of which are well preserved. Specimens were found at Pinhay Bay (*laqueus–conybeari* and *bucklandi* subzones); Long Itchington (*laqueus, extranodosa/complanata* and *bucklandi?reynesi* subzones); Maisemore (*rotiforme* subzone) and Hock Cliff (*bucklandi* subzone).

Diagnosis. Round wheels with small teeth on the edge of the inner rim, a median ridge along the ventral surface of each spoke and a smooth, flat hub on the ventral side.

Dimensions. Diameter of 75–405 μm (*n* = 85); relative diameter of the hub from less than 20% to more than 40% of the wheel diameter but typically 25–35%; number of spokes 7–15.

Description. Round, occasionally polygonal wheels (Pl. 3, figs 7, 11). Outer rim may be undulating (Pl. 3, fig. 8) with the outward-facing convex part corresponding to the interspoke space. Inner edge of the rim usually bears a variable number of blunt-ended teeth (Text-fig. 12; Pl. 3, fig. 15). Rare examples are found in which the whole rim appears to be smooth (Pl. 3, fig. 10). Spoke number ranges from 7 to 15, predominantly 10–13 (see Text-fig. 13). The spokes are strongly arched (Pl. 3, fig. 12) and straight (Pl. 3, fig. 9) or slightly wider in the middle (Pl. 3, fig. 8). Width of the spokes is dependent on their number, but is normally relatively thin. In most specimens there are median ridges along the ventral surface of the spokes (Pl. 3, fig. 8). The ridges are confluent with the hub rather than detached from it to form a 'star'. The ventral surface of the hub is flat and lies below the plane of the rim (Pl. 3, fig. 12). On the dorsal side the hub is rounded to flat and lies in a plane below, or more commonly above, that of the rim (Pl. 3, fig. 13). Ontogenetic stages show strongly tapering spokes which must thicken later in development (Pl. 3, fig. 14).

TEXT-FIG. 13. Frequency distribution of spoke number in the specimens of *T. synapta* used in Text-figure 11.

Theelia synapta
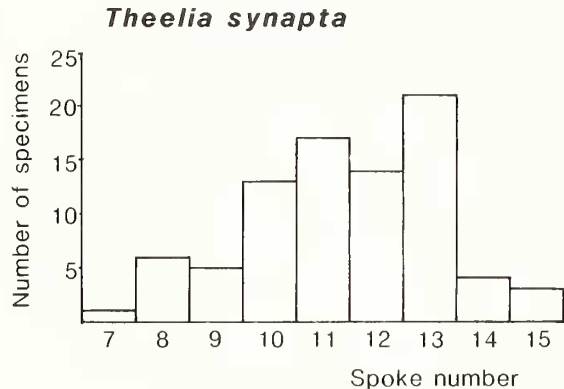
Discussion. The significance of various wheel parameters, particularly teeth and a central star, are discussed elsewhere (Gilliland 1990). Teeth are often difficult to recognize or appear to be missing in some parts of the rim due to poor preservation. Hence, the presence/absence of teeth may not be a reliable character. However, detailed observation of many specimens, preferably by scanning electron microscopy, should be sufficient to determine whether teeth are consistently absent or not.

A number of previously described wheels with smooth inner rims are similar to *Theelia synapta*. The most similar is *T. immissorbicula* Mostler which is widely distributed in the Upper Triassic (Gilliland 1990). Mostler (1972a) also includes *T. immissorbicula* in a list of Jurassic taxa but there is no indication of the original record. *T. germanica* Kozur, a probable synonym of *T. immissorbicula*, is known from the Lower-?Upper Triassic (Kozur 1969; Soodan 1986). In these two species, however, the inner edge of the rim is consistently smooth and neither has a median ridge on the spokes.

There is a negative correlation between the number of spokes and wheel diameter (Text-fig. 11) as is found in elasipod wheels, but Pawson (1971) found no such correlation amongst synaptid wheels of the giant larva *Auricularia nudibranchiata*. There is also a positive correlation between the number of teeth and diameter (Text-fig. 12) as Zankl (1966) found in *Theelia seniradiata*. Thus the relative number of teeth is a more important character than the absolute number.

The most similar Recent sclerites to *Theelia synapta* are the wheels found in the larvae of the Synaptidae (order Apodida). *T. synapta* is therefore referred to the Synaptidae but, because no anchors or anchor-plates, the sclerites of adult synaptids, have been found in the Blue Lias, it may be considered to be a stem-group synaptid. *T. synapta* differs from Recent synaptid wheels in having a ridge on the spokes and a correlation between diameter and number of spokes.

Family ACHISTRIDAE Frizzell and Exline, 1955

Included genus. Achistrum Etheridge.

Stratigraphic range. Middle Devonian to Lower Cretaceous (or Palaeocene?).

Diagnosis. Hook-shaped sclerites with an eye (terminal loop), shank and spear.

Remarks. Hampton (1958*b*) recognized four subgenera of *Achistrum* based on the structure of the eye. Frizzell and Exline (1966) dismissed three of these, as discussed in more detail in Gutschick *et al.* (1967), but raised a fourth, *Aduncrum*, to generic level. However, *Aduncrum* was based on a single specimen found in association with undoubted species of *Achistrum* and is simply an aberrant/broken specimen (personal observation) as suggested by Rioult (1961). Beckmann (1965) erected a new subgenus *Porachistrum* for hooks with a sieve-like partition in the eye. However, Gutschick *et al.* (1967) recovered similar forms (*Achistrum coloculum*) in association with hooks with a more typical eye and did not consider this character merited a separate subgenus.

The family certainly extends as far as the Lower Cretaceous (e.g. Kubiatowicz and Matyja 1977). *Achistrum* was reported by Soodan (1972) from the Palaeocene of India but without a description or figures. Given its significance to the stratigraphic range of the family the Indian record is only tentatively accepted until more details are available.

Genus ACHISTRUM Etheridge, 1881 emend Frizzell and Exline, 1955

Type species. Achistrum nicholsoni Etheridge, 1881.

Diagnosis etc. As for family.

Achistrum monochordata Hodson, Harris and Lawson, 1956

Plate 4, figs 1–8

1905   *Uncinulina polymorpha* Terquem; Hucke, p. 167, pl. 23, fig. 6*a* (only).
1935   'Holothurien-Kalkkorperchen' Eichenberg, p. 318, text-fig. 1 (four specimens top right only).
1936   'Angelhaken' Bartenstein, pp. 1–2, text-figs 1*a*–*c*, 6.
1938   Unidentified sclerites Wicher, pls 1–2 (*pars*), 5 (*pars*).
1955   *Achistrum bartensteini* Frizzell and Exline, p. 94, pl. 4, figs 5–7.
1955   *Calcligula? huckei* (in part) Frizzell and Exline, p. 70, pl. 1, fig. 28.
1956   *Achistrum monochordata* Hodson, Harris and Lawson, pp. 340–341, text-figs 10–11.
1957   *Achistrum monochordata* Hodson, Harris and Lawson; Hampton, p. 509, text-figs 6–8.
1958   *Achistrum monochordata?* Hodson, Harris and Lawson; Summerson and Campbell, p. 968, pl. 125, figs 3–7.
1958   *Achistrum bartensteini* Frizzell and Exline; Said and Barakat, p. 268, pl. 6, figs 1–5.
1961   *Achistrum monochordata* Hodson, Harris and Lawson; Rioult, pp. 139–140, pl. 1, fig. 2.
1962   *Achistrum monochordata* Hodson, Harris and Lawson; Fletcher, p. 325, text-figs 6–7.
1962   *Achistrum bichordata* Fletcher, p. 323, text-figs 1–2.
1967   *Achistrum monochordata* Hodson, Harris and Lawson; Garbowska and Wierzbowski, pp. 530–531, text-fig. 4A–M.
1967   *Achistrum monochordata* Hodson, Harris and Lawson; Gutschick, Canis and Brill, p. 1471, pl. 187, fig. 30.
1967   *Achistrum bartensteini?* Frizzell and Exline; Gutschick, Canis and Brill, p. 1470, pl. 187, fig. 32.
1968*a* *Achistrum bartensteini* Frizzell and Exline; Mostler, p. 14, pl. 2, figs 7–8.
1969   *Achistrum monochordata* Hodson, Harris and Lawson; Gorka and Luszczewska, pp. 382–383, pl. 79, figs 2–6.
1971   *Achistrum monochordata* Hodson, Harris and Lawson; Zawidzka, p. 434, pl. 1, fig. 7; text-fig. 2.

1973   *Achistrum monochordata* Hodson, Harris and Lawson; Michelson, p. 60, pl. 2, figs 1, 9; pl. 3, fig. 7.

1976   *Achistrum* cf. *monochordata* Hodson, Harris and Lawson; Mostler and Rahimi-Yazd, pp. 12–13, pl. 3, fig. 18.

1976   *Achistrum monochordata* Hodson, Harris and Lawson; Gheorghian, pp. 59–63, pl. 2, figs 1–2.

1977   *Achistrum monochordata* Hodson, Harris and Lawson; Mirauta and Gheorghian, p. 156, no figure.

1977   *Achistrum monochordata* Hodson, Harris and Lawson; Soodan, p. 102, pl. 1, fig. 4.

1977   *Achistrum monochordata* Hodson, Harris and Lawson; Kubiatowicz and Matyja, p. 402, text-fig. 1*a–b*.

1978   *Achistrum monochordata* Hodson, Harris and Lawson?; Copestake, pl. 32, fig. 6.

1986   *Achistrum bartensteini* Frizzell and Exline; Kristan-Tollmann (in Fischer *et al.*), p. 131, pl. 29, fig. 2.

1987   *Achistrum monochordata* Hodson, Harris and Lawson; Soodan and Whatley, p. 169, pl. 1, figs L–M, R–S.

1987   *Achistrum bichordata* (Fletcher); Soodan and Whatley, p. 168, pl. 1, fig. F.

Types. Holotype, J. 35785; paratype, J. 35784; Upper Jurassic, Lower Oxfordian (*cordatum* zone), Redcliff, near Weymouth, Dorset, housed in the Sedgwick Museum, Cambridge.

Material studied. More than 2200 specimens including BMNH E27120–27129, E27133–27140, E27207, and E27260–27263. Specimens are recorded from every sub-zone sampled in the period *johnstoni–scipionianum*, and from all four Blue Lias localities.

Stratigraphic range. Lower Carboniferous to Lower Cretaceous.

Diagnosis. Species of *Achistrum* with one or more undivided cross-bar(s) within the eye.

Dimensions. Length 137–845 μm (mean = 339 μm, n = 201). Width 35–220 μm (mean = 106 μm, n = 1200). The maximum diameter of the shaft near to the head is typically 35–40 μm in larger specimens.

Description. Hooks with a single bar across the eye or rarely with two bars on either side of the eye (Pl. 4, fig. 2). Occasionally the bar is broken in the mid-region to produce 'thorns' (Pl. 4, fig. 8). Almost all hooks exhibit eccentricity which is variable (cf. Pl. 4, figs 4–5). Left- and right-handed specimens are equally common. The head of the hook is usually obviously wider than the shaft and angled slightly in the direction of the spear (Pl. 4, fig. 7). The eye occupies the central and eccentric area of the head and consequently the head is often thicker on the non-eccentric side (Pl. 4, fig. 4). The bar varies in position from subcentral to almost fused with the edge but always on the eccentric side. Between the eye and the spear the shank is usually curved (Pl. 4, fig. 7) although this may be slight. The sharply angled spear is relatively short, compared to the shank, and thins to a sharp point, although exceptions occur (Pl. 7, figs 1, 6). The shaft is typically oval in cross-section (parallel to the plane of the long axis) becoming more circular, and wider, towards the head.

Discussion. The relative importance given to characters for classifying hooks has been discussed extensively (Hampton 1957; Rioult 1961; Garbowska and Wierzbowski 1967; Gutschick *et al.* 1967). Details of the head and eye should be given prominence because these are the most distinctive and easily recognized characters. Characters other than the eye can be useful, however, particularly where poor preservation masks details of the eye. *Achistrum issleri*, which has an empty eye, differs from *A. monochordata* in its circular cross-section and centrally placed (non-eccentric) head. In *A. monochordata* the eye of smaller specimens is commonly infilled but other characters are similar to larger specimens, and, in addition, many small hooks possess a bar (Pl. 4, fig. 3). Rare odd forms (e.g. Pl. 4, fig. 6) should be regarded as aberrant specimens rather than the basis for new morphospecies (e.g. *A. britannica* and *A. warboysensis* Soodan and Whatley 1987). Examples in which the bar has broken, to produce 'thorns', originally assigned to *A. bartensteini*, were correctly synonymized with *A. monochordata* by Rioult (1961).

Hooks with two bars in the eye referable to *A. bichordata* Fletcher, 1962 are infrequent in the present material. Fletcher noted that *A. monochordata* was the commonest morphospecies in his

material. Thus *A. bichordata* is probably a morphological variant forming a small percentage of any normal population of *A. monochordata*. Fletcher recorded other rare hook morphospecies but none was found in the Blue Lias material. Richardson (personal communication in Pawson 1980) noted from body fossil material that more than ten 'species' (= morphospecies) of hooks could be found in one individual. This, together with the distribution of *A. monochordata* and '*A. bichordata*', suggests that biological species possess different morphospecies of *Achistrum* but vary in respect of the dominant type. It is therefore useful to recognize forms of morphospecies, equivalent to former morphospecies, i.e. 'single barred' and 'double barred' forms of *A. monochordata* and to determine the predominating hook type using a large sample. It is possible that the relative size of hooks, e.g. length/width, differs between species. Although there are two distinct size groupings in Text-figure 5, these are unlikely to represent two different species because of the strong correlation between length and width at all sizes (see Text-fig. 4).

Order UNCERTAIN – DENDROCHIROTIDA Grube, 1840 or MOLPADIIDA Haeckel, 1896
[Parafamily PRISCOPEDATIDAE Frizzell and Exline 1955] *pars*
Genus STAUROCUMITES Deflandre-Rigaud, 1952 emend

Type species. Staurocumites bartensteini Deflandre-Rigaud, 1952.

Diagnosis. Tables with a base of four perforated arms arranged in a cross. Additional holes of equal or smaller size to those in the arms may form between the arms. The spire projects from the centre and is solid with a quadripartite base.

Discussion. The genus appears to be monospecific. Mortensen (1937) considered *S. bartensteini* to be derived from either of the Recent orders Aspidochirotida or Dendrochirotida, but without elaborating. However, this morphospecies appears to have affinities with tables found in both the Recent order Dendrochirotida and the family Molpadiidae (order Molpadiida) (Gilliland 1990).

Staurocumites bartensteini Deflandre-Rigaud, 1952

Plate 4, figs 9–16, 21

1936   Glitter-Plättchen in Kreus-Form Bartenstein, pp. 8–9, text-figs 4*a–c*, 5, 12.
1937   Spicule of holothurian Mortensen, pp. 26–27, pl. 4, fig. 10.
1952   Unnamed crosses Fischer, text-fig. 19-2–8.
1952   *Staurocumites bartensteini* Deflandre-Rigaud, p. 6.
1953   *Staurocumites bartensteini* Deflandre-Rigaud; Deflandre-Rigaud, p. 953, text-fig. 12.
1955   *Priscopedatus bartensteini* (Deflandre-Rigaud); Frizzell and Exline, pp. 103–104, pl. 5, figs 4, 6–9.
1961   *Staurocumites bartensteini* Deflandre-Rigaud; Rioult, pp. 140–141, table 1, figs 10, 18.
1964   *Priscopedatus bartensteini* (Deflandre-Rigaud); Zankl, pl. 1, fig. 3*f*.
1966   *Staurocumites* cf. *bartensteini* Deflandre-Rigaud; Zankl, pp. 76–77, pl. 5, fig. 3.
1966   *Staurocumites bartensteini* Deflandre-Rigaud; Frizzell and Exline, p. U667, text-fig. 532(5).
1968*a*   *Priscopedatus* cf. *normani* Schlumberger; Mostler, text-fig. 5(2).
1968*b*   *Priscopedatus acanthicus* Mostler, pp. 14–15, pl. 3, fig. 1; text-fig. 1.
1968*b*   *Priscopedatus staurocumitoides* Mostler, pp. 17–18, pl. 3, figs 2–5; text-fig. 2*a–d*.
1968*b*   *Staurocumites bartensteini* Deflandre-Rigaud; Mostler, pp. 31–32, pl. 3, figs 6–9; text-fig. 2*a–c*.
1968*b*   *Staurocumites horridus* Mostler, pp. 22–23, pl. 3, fig. 10.
1968*c*   *Staurocumites bartensteini* Deflandre-Rigaud; Mostler, p. 56, pl. 1, figs 4–5.
1968   *Staurocumites bartensteini* Deflandre-Rigaud; Speckmann, p. 204, pl. 1, fig. 9.
1968   *Priscopedatus* sp. 1 Speckmann, p. 202, pl. 1, figs 1, 3.
1971   *Staurocumites barensteini* Deflandre-Rigaud; Zawidzka, p. 436, pl. 2, figs 2–5.
1971   *Priscopedatus staurocumitoides* Mostler; Kozur and Mostler, p. 27.
1971   *Staurocumites bartensteini* Deflandre-Rigaud; Kozur and Mostler, p. 27.

1972   *Priscopedatus acanthicus* Mostler; Kozur and Mock, pl. 6, figs 28–29; also *P.* cf. *acanthicus*, pl. 6, fig. 27.
1972   *Priscopedatus staurocumitoides* Mostler; Kozur and Mock, pp. 13–14, pl. 6, figs 17–22.
1972   *Priscopedatus bartensteini* (Deflandre-Rigaud); Kozur and Mock, pl. 6, figs 12–14.
1972   *Priscopedatus horridus* (Mostler); Kozur and Mock, pl. 6, figs 25–26.
1972   *Staurocumites bartensteini* Deflandre-Rigaud; Mostler, p. 8 (listed only).
1973   *Priscopedatus staurocumitoides* Mostler; Mostler and Parwin, p. 12 (listed only).
1973   *Staurocumites bartensteini* Deflandre-Rigaud; Mostler and Parwin, p. 12 (listed only).
1974   *Priscopedatus acanthicus* Mostler; Kozur and Mock, pl. 6, figs 4–5.
1974   *Priscopedatus staurocumitoides* Mostler; Kozur and Mock, pl. 6, figs 1–2.
1974   *Priscopedatus bartensteini* (Deflandre-Rigaud); Kozur and Mock, pl. 5, figs 12–13.
1974   *Priscopedatus horridus* (Mostler); Kozur and Mock, pl. 5, figs 14–15.
1977   *Priscopedatus staurocumitoides* Mostler; Mirauta and Gheorghian, p. 156, pl. 14, figs 1–2, 4, 9.
1977   *Priscopedatus horridus* (Mostler); Mirauta and Gheorghian, p. 156, pl. 14, fig. 3.
1980   *Staurocumites bartensteini* Deflandre-Rigaud; Donofrio *et al.*, p. 68 (listed only).
1986   *Staurocumites bartensteini* Deflandre-Rigaud; Kristan-Tollmann, pp. 131–132, pl. 29, figs 4–9.

Types. The holotype and paratypes were selected by Deflandre-Rigaud (1952), and the holotype figured by her (1953, p. 953, fig. 12), based on material originally described by Bartenstein (1936, figs 4*a, c*, 5, 12) from the Pliensbachian of Hambuhren (N. Germany).

Material studied. More than 300 specimens including BMNH E27198–27206, E27209–27221, E27223–27227, E27229 and E27264–27266, from Maisemore Cliff (*rotiforme* subzone), Hock Cliff (*bucklandi* subzone) and Long Itchington (*laqueus, extranodosa/complanata, rotiforme* and *bucklandi*?*reynesi* subzones).

Stratigraphic range. Middle Triassic (Anisian) to the Lower Jurassic (Pliensbachian).

Diagnosis. As for genus.

Dimensions. Maximum diameter, 100–255 μm (average of *x* and *y*, 105–245 μm); maximum width of arms, 25–56 μm (average arm width, 28–52 μm), see also Text-figure 14; spire height is normally *c.* 40–50% of the diameter.

Description. Tables usually with a quadripartite base composed of four arms each with an elongate hole. Rare examples have additional holes between the main ones (Pl. 4, fig. 9). Other rare forms include three-armed (Pl. 4, fig. 13) and five-armed (Pl. 4, fig. 14) specimens. Length and width of the arms are variable (Text-fig. 14; Pl. 4, figs 11, 15), even within the same specimen and irregularly shaped base plates occur (Pl. 4, fig. 16). The spire is vertical and relatively short but often broken near to the base. One odd example was found with a relatively long spire bent over at the top (Pl. 4, fig. 12). The base of the spire is solid with four faint sloping ridges at the junctions of the arms (Pl. 4, fig. 10). The spire narrows towards the top (Pl. 4, fig. 10) and terminates in three diverging thorns or spines.

Discussion. *S. bartensteini* is a distinctive and widely reported morphospecies. Previous authors have also noted a wide variation in shape (e.g. Mostler 1969, 1972*b*). Rioult (1961) suggested that different forms may be of stratigraphic use, at least in the Lias. This is unlikely since a wide range exists even in specimens from the same sample (Text-fig. 14).

Mostler (1968*a*) erected a new species, *Priscopedatus staurocumitoides*, distinguished from *S. bartensteini* on the presence of more than two (usually three to six) additional holes on the arms, despite showing that the two species simply form a morphological growth series (Text-fig. 2*a–f*). Kozur and Mock (1972, 1974) record both *S. bartensteini* and *P. staurocumitoides* from the Upper Illyrian (Anisian, Middle Triassic) of the same locality. In the present material there were rare examples of '*P. staurocumitoides*'. Clearly the two morphospecies are synonymous.

Mostler (1968*a*) described two other new species *Staurocumites horridus* and *Priscopedatus acanthicus*, both from the same locality as *P. staurocumitoides*. *S. horridus* is differentiated on its thick base plate (i.e. small holes), massive spire and spiny periphery. However, the thickness of the base plate varies in *S. bartensteini* (see Pl. 4, fig. 11) and in *S. horridus* itself (Kozur and Mock 1972,
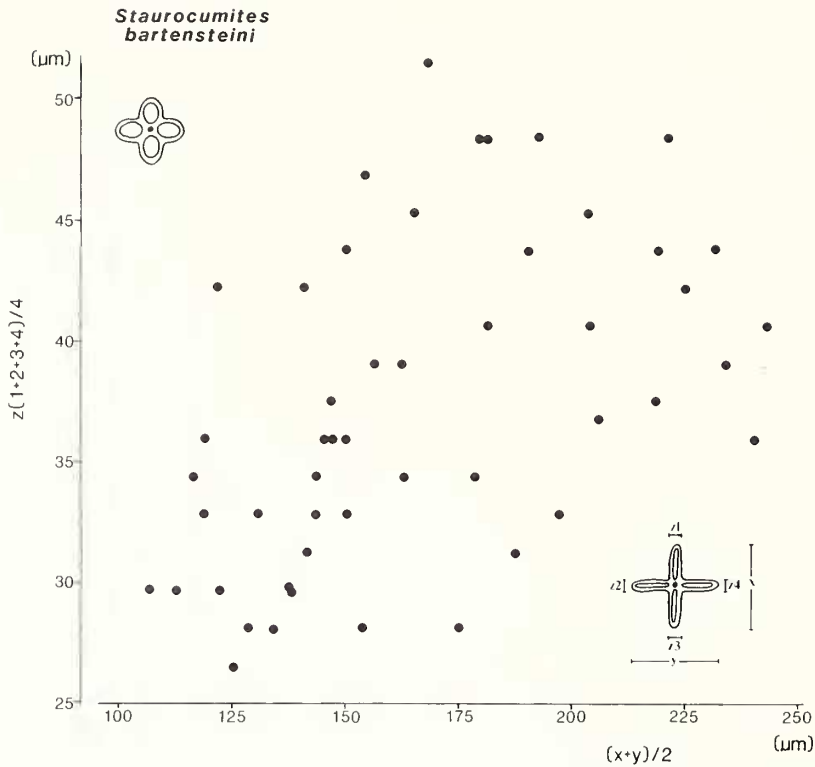
TEXT-FIG. 14. A plot of the average arm length against average arm width of *S. bartensteini* from sample M3 (*n* = 50).

pl. 6), the spire of *S. horridus* looks no different from that of *S. bartensteini*, and the spiny edge is indicative of continuing growth at the periphery. *P. acanthicus* is simply a form of *S. horridus* in which secondary holes have developed. In addition all these morphospecies have been recorded from the same sample (Kozur and Mock 1974). Mostler (1972*b*) noted the obvious similarity between *S. bartensteini*, *P. staurocumitoides* and *P. acanthicus*, but did not propose any synonymy. The available evidence indicates that *S. horridus* and *P. acanthicus* are also synonyms of *S. bartensteini*.

Kristan-Tollmann (1986) included *Priscolongatus* Gorka and Luszczewska within *Staurocumites*, based on its resemblance to aberrant forms of *S. bartensteini*. This synonymy is questionable since the arms of *Priscolongatus* are solid with holes restricted to the central area, which is concavo/convex rather than flat, and its spire is short and conical, composed of fused pillars, unlike that of *Staurocumites*. *Priscolongatus*, which may extend back to the Middle Triassic, is possibly closely related to *Staurocumites* (Gilliland 1990).

Order UNCERTAIN – DENDROCHIROTIDA Grube or MOLPADIIDA Haeckel
Parafamily PUNCTATITIDAE Mostler and Rahimi-Yazd, 1976

Included genera. *Punctatites*, *Uncinuloides* in part.

Diagnosis. Rod-shaped sclerites with a perforated or non-perforated central area which is commonly the widest part of the rod (occasionally additional arms develop from the central area).

In extreme forms the central area is a short, narrow rod connecting the two wider arms. Some form of slit occurs at either end or over the entire length of the sclerite.

Remarks. The classification, morphological variation and affinities of the Punctatitidae are discussed in detail in Gilliland (1990). *Punctatites* was originally included in the parafamily Stichopitidae and then placed in a separate family. Also included in the new family was the genus *Uncinuloides*. Kozur and Mock (1972), in an extensive revision of *Punctatites*, synonymized *Uncinuloides* with this genus, and certainly a few previously recognized morphospecies, such as *U. diffisus* Mostler, 1971, overlap with taxa previously assigned to *Punctatites*. On the other hand, as discussed in Mostler and Rahimi-Yazd (1976), some other forms of *Uncinuloides* show a morphological gradation with *Uncinulina*, a genus based on rods that may be confused with spicules of non-holothurian groups (Gilliland 1990). Hence, only some species of *Uncinuloides* can be accepted as holothurian sclerites, whilst others may be placed in *Punctatites*.

Genus PUNCTATITES Mostler, 1968 emend Kozur and Mock, 1972

Type species. Punctatites longirameus Mostler, 1968c.

Diagnosis. Rods of the Puncatititidae with a smooth edge, usually a prominent perforated slit, and no development of a perforated eccentric area.

Punctatites? aff. extensus (Mostler 1968c)

Plate 4, fig. 23

1968b   *Binoculites extensus* Mostler, pp. 429–430, pl. 1, figs 1–2.
1972   *Punctatites extensus* (Mostler); Kozur and Mock, pl. 15, figs 8–9.
1972a   *Punctatites extensus* (Mostler); Mostler, p. 4 (listed only).
1973   *Binoculites extensus* Mostler; Kozur and Mostler, p. 307 (listed only).
1973   *Punctatites extensus* (Mostler); Mostler and Parwin, p. 12 (listed only).
1979   *Punctatites extensus* (Mostler); Mostler, p. 336 (listed only).

Types. Holotype and paratype from the Upper Triassic, Middle Norian, of Sandling (Northern Calcareous Alps, Austria).

Material studied. One specimen (E27222) from L18e, *angulata* zone of Long Itchington.

Stratigraphic range. Upper Triassic (Middle Norian) to Lower Jurassic.

Diagnosis. A straight form of *Punctatites* with a thin, imperforate mid-region.

Dimensions. Length, 900 μm; width at the mid-point, 55 μm; maximum width at the expanded end, 110 μm.

Description. Large rod-shaped sclerite with a narrow middle region (nearly half of the total length) and at either end an elongate expanded area. At one end, which is slightly broken, the sides of the widened area are parallel whilst the other end is ellipsoidal. Within each expanded part there is a sunken area which at the broken end, at least, appears to be perforated.

Discussion. The specimen is slightly broken and the grooved areas at either end are infilled with matrix, obscuring details. However, the presence of a hole at the broken end suggests that the grooved areas are perforated and the sclerite is tentatively referred to *Punctatites*. There are a number of morphospecies of *Punctatites* of which *P. extensus* is the most similar to the example described here. Although the relative length of the central area is variable in *P. extensus*, in forms

in which this is large the rod is thinner than in the specimen described (see, for example, Mostler 1968b, pl. 1, fig. 1), and hence assignment to *P. extensus* is tentative until further Blue Lias examples are found.

The affinities of *Punctatites* are uncertain, but probably lie with either the Dendrochirotida or Molpadiidae.

Order UNCERTAIN

[Parafamily PRISCOPEDATIDAE Frizzell and Exline 1955]

Priscopedatus sp. nov.?

Plate 4, figs 18, 24, Plate 5, figs 1–2

Types. One specimen, the holotype (BMNH E27342), from the *liasicus* (*laqueus?*) zone, Long Itchington.

Diagnosis. A table with a round base plate in which two irregular circles of variably shaped holes surround a large central hole. The spire is hollow and formed from four vertical pillars. At the top a Maltese-cross arrangement of spines overhangs the large central hole (Pl. 5, fig. 2).

Dimensions. Diameter, 80 μm; spire height, 40 μm.

Description. Small, circular table with undulating periphery imparting a spiny effect. In the centre of the base is a large hole surrounded by an estimated eight small holes (Pl. 4, fig. 18). Around the outer part are fifteen to sixteen irregularly arranged holes of variable size and shape but mostly larger than those in the inner circle. Viewed from above the large central hole and inner circle of small holes are obscured by the spire. There are a few tiny holes situated at the periphery between the larger holes (Pl. 4, fig. 18). The spire is shorter than the diameter of the disc and formed from four pillars connected midway up by cross-bars (Pl. 4, fig. 24). At the top of the spire are three layers of spines spread outwards, the lower of which forms a Maltese-cross shape.

Discussion. This is a generalized four-pillared type of table. Fossil examples are not common possibly because of their small size (frequently less than 100 μm in diameter). Deflandre-Rigaud (1962) has described a number of such examples from the Oxfordian of France, the most similar of which are *Priscopedatus heteroporus*, *P. affinis* and *P. spiniferus*. The former has irregularly distributed outer holes, as in the present specimen, but only one circle of these and, in addition, there is a large central hole unobscured by the spire. *P. affinis* differs in having four central holes and only eight large regularly arranged holes around these. *P. spiniferus* also has four central holes, a square-shaped base plate and only one circle of large holes. Because of these differences the present specimen is assigned to a new species. However, due to the poor preservation, and the fact that there is only one specimen, the species is left under open nomenclature until further material is found.

Four-pillared tables are widespread amongst holothurian families (Gilliland 1990). The presence of two circles of holes and the variable size, shape and distribution of the outer holes are characters most frequently found in the tables of dendrochirotes, but may also occur in aspidochirotes. Tables of this kind typically form assemblages with a variety of other sclerite morphotypes but no such association can be identified because of its rarity. Earlier records of four-pillared tables include

EXPLANATION OF PLATE 5

Figs 1–2. *Priscopedatus sp. nov.?* Holotype; E27342; L9b; *laqueus?extranodosa/complanata* subzone, both × 580.

Figs 3–5. Calcareous ring Type 1 interradials. 3, E27435; L16e; *angulata* zone, × 85. 4–5, E27424; H23; *bucklandi* subzone, × 70, × 130, respectively.

Figs 6–10. Calcareous ring Type 1 radials. 6, E27419; H19; *bucklandi* subzone, × 105. 7, E27430; H4; *bucklandi* subzone, × 55. 8, E27417; H19; *bucklandi* subzone, × 55. 9, E27416; H19; *bucklandi* subzone, × 55. 10, E27437; H15; *bucklandi* subzone, × 55.

PLATE 5
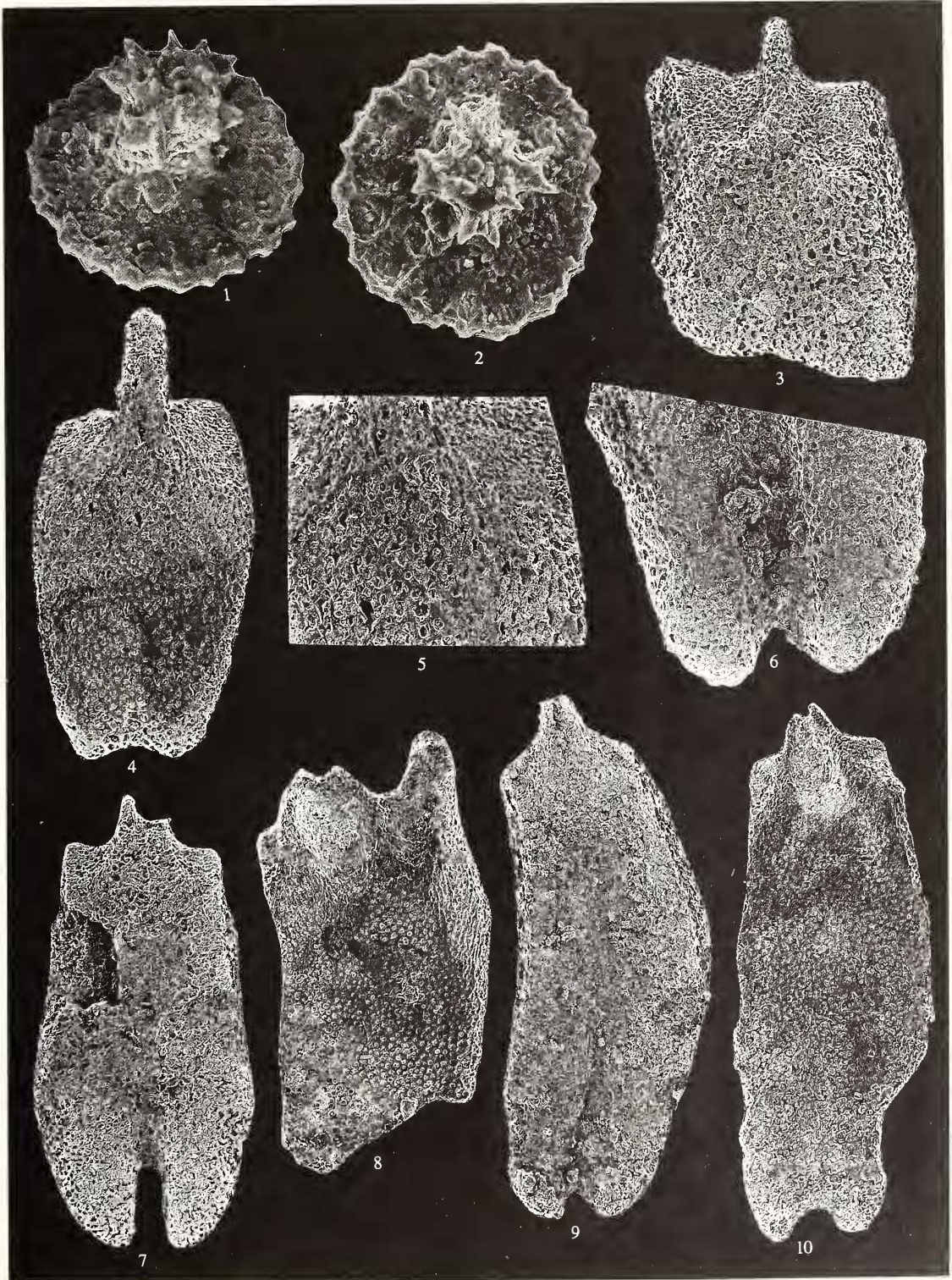
GILLILAND, Blue Lias holothurian sclerites

Priscopedatus quinquespinosus Mostler and Rahimi-Yazd, 1976, from the Upper Permian, *P. procerus* Mostler, 1971, from the Middle Triassic, and *Solopedatus parvus* Mostler, 1971, from the Upper Triassic, but these are atypical. The latter, for example, resembles the reduced tables of the Recent genus *Labidodemas*. *Priscopedatus* sp. nov.? is the earliest typical example with a prominent four-pillared spire.

GENERAL DISCUSSION

Sorting and preservation

There is little information on the fate of sclerites following death. The rate at which dermal tissue decomposes varies between different holothurians (Schäfer 1972; Pawson 1980; Gilliland 1990). Frizzell and Exline (1955) concluded that most sclerites were deposited near to where the animal lived and the non-holothurian fauna in the present material is generally consistent with this conclusion. For example, various echinoid or ophiuroid elements commonly occur in the same sample. Hallam (1960) concluded that the Blue Lias fauna contains a mixed life and indigenous death assemblage through much of the succession, i.e. a limited taphonomic loss of faunal components but some disturbance following death.

The distribution of elements of the calcareous ring relative to their associated sclerite morphotypes suggests some dispersal took place after death. An absence/scarcity of morphotypes expected to co-occur with *Binoculites*, i.e. dendrochirote rods (Gilliland 1990) or tables, may also indicate differential sorting of sclerites. However, the differences between these various morphotypes are slight and seem unlikely to be significant enough to affect sorting.

Evidence from size frequency distributions is also limited. The length of buttons from the Recent species *Pawsonia saxicola* shows a near normal distribution (Gilliland 1990) and Hampton (1959) obtained a similar result for the buttons of *Holothuria impatiens*. The only information on the expected distribution of hook size is in Sroka (1988) who found a bimodal distribution with a higher peak of smaller specimens. In the Blue Lias material there is no apparent correlation of changes to these predicted size frequencies, as a consequence of sorting, for *Achistrum monochordata* or *Binoculites terquemi* from the same samples (compare Text-fig. 6b–d, with 6f–h).

Palaeogeography

The present investigation, together with previous records (e.g. Blake 1876; Copestake 1978), shows that holothurians were distributed across southern Britain in an area which today extends from Dorset north to Yorkshire, and westward to the Irish Sea. A comparison of the main components of the British Blue Lias fauna with Hettangian and Sinemurian records from Denmark, France and Germany indicates a similar association of sclerites is found across north-west Europe; this also persists through much of the Lias. *Binoculites germanica*, particularly the form Calclamna, and hooks are the most widespread and common. There is, however, regional variation. In Denmark and Britain *Achistrum monochordata* occurs in isolation, whereas in France and Germany *A. issleri* and *A. monochordata* occur together. In Denmark *A. monochordata* comprises only about 25% of sclerites (with 75% *Binoculites* form Calclamna) compared with a significantly higher proportion (c. 49%) in southern Britain. *Staurocumites bartensteini* is widespread but less common in the Lias


EXPLANATION OF PLATE 6

Fig. 1. Calcareous ring Type 1 radial. E27419; H19; *bucklandi* subzone, × 105.
Figs 2, 4–5, 8–10. Calcareous ring Type 2. 2, 5, E27423; L9b; *laqueus?extranodosa/complanata* subzone, × 145. 4, E 27421; L9b; *laqueus?extranodosa/complanata* subzone, × 130. 8–9, E27422; H15; *bucklandi* subzone, × 145, × 160, respectively. 10, E27440; L41b; *bucklandi?* subzone, × 100.
Figs 3, 6. Calcareous ring Type 3. E27426; H15; *bucklandi* subzone, both × 85.
Fig. 7. Calcareous ring Type 4. E27427; L42b; *bucklandi?reynesi* subzone, × 115.

PLATE 6
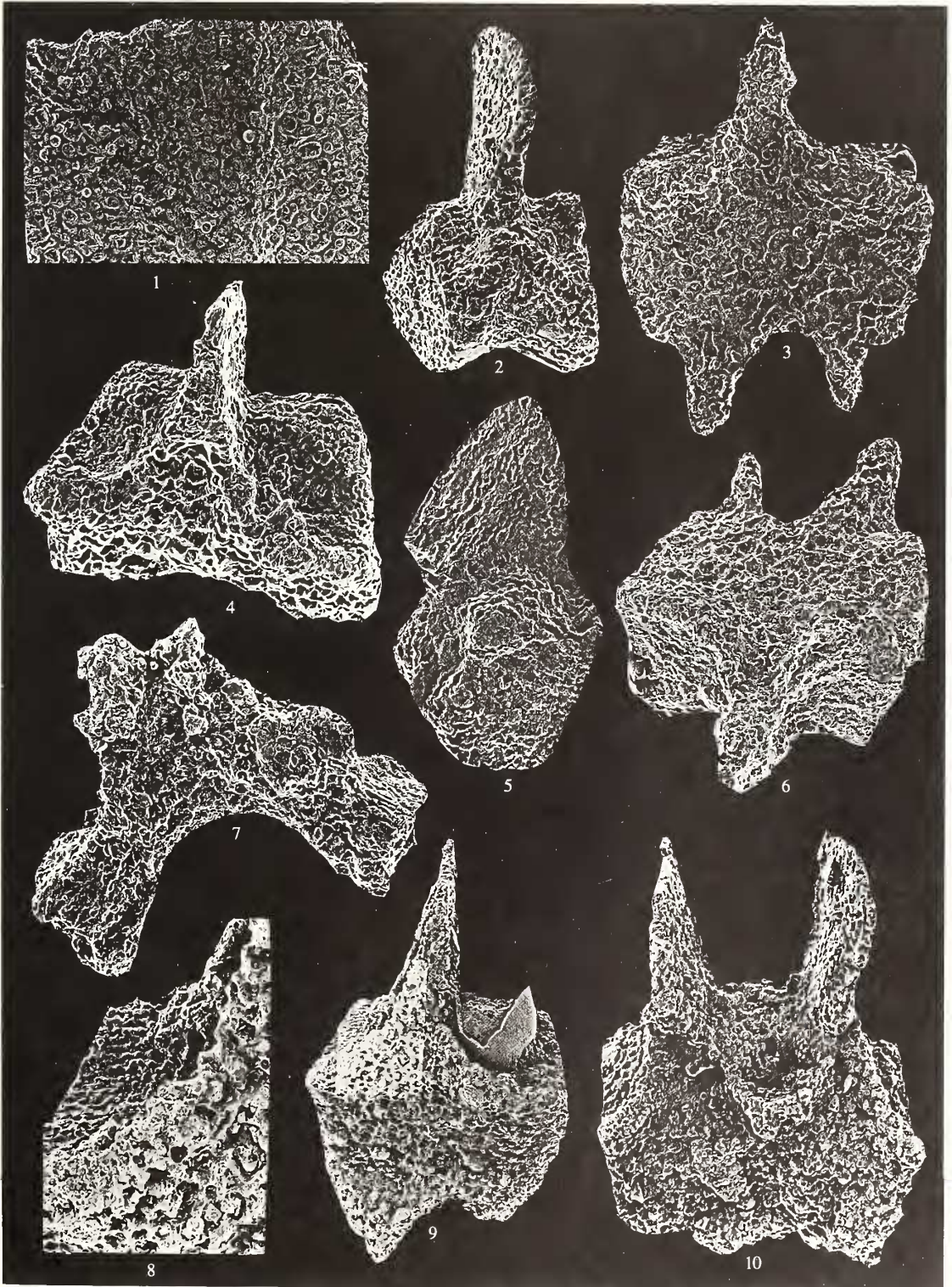
GILLILAND, Blue Lias holothurian sclerites

of both Britain and other regions of Europe. Partly formed *Binoculites jurassica* has a similar geographical range to *B. terquemi* but is less frequent. Fully formed *B. jurassica* have been found only in Denmark and Britain, but the British specimens are more clearly differentiated from fully developed *B. terquemi*. The most significant character of the British holothurian fauna is the presence of wheels which elsewhere in Europe only appear higher up in the Lias (?Sinemurian, Pliensbachian). Thus the southern British fauna included a high proportion of *A. monochordata*, a well developed *B. jurassica* assemblage and the presence of chiridotids and synaptids, compared to other regions. The latter two may indicate a more on-shore assemblage in southern Britain during this period.

Palaeoenvironment

The holothurian fauna from the Blue Lias is quite diverse. Comparison with the distribution of Recent taxa for palaeoenvironmental analysis is limited by the uncertain affinities of some of the morphotypes and the difficulty of restricting others to a taxonomic level below that of a Recent family. Considering the affinities of the fauna, e.g. *Palaeoypsilus* with the Ypsilothuriidae, or *Theelia convexa* and *T. synapta* with the Chiridotidae and Synaptidae respectively, it can be concluded only that the holothurian fauna does not undermine the environmental interpretation of the Blue Lias, i.e. that it was deposited in shallow (no deeper than 150 m), warm (modern tropical–subtropical temperatures) water (Hallam 1960). It is probable, however, that the holothurian fauna from the Blue Lias was composed of a mixture of predominantly shallow water taxa at the lower limit of their distribution and less common deeper water species near to their upper limit.

Holothurians from the Blue Lias have a varied ecology. Dendrochirotes are suspension feeders which either extend their dendritic tentacles from a burrow or cling to a hard/seaweed substratum. Dactylochirotes burrow into unconsolidated sediments feeding on detrital material whilst elasipods plough through the sediment surface. Molpadiids burrow into soft mud and apodans (Chiridotidae and Synaptidae) are commonly burrowers. The activities of the burrowers, particularly vagile chiridotids, would have contributed to disruption of the sediment.

Biostratigraphic aspects

Rioult (1961) proposed a zonation of the whole Lias based on twenty-eight holothurian morphospecies, some apparently with a limited vertical range. The morphospecies were grouped into three associations which defined the Hettangian–Sinemurian, the Pliensbachian–lower Toarcian (*tenuicostatum* subzone) and the middle–upper Toarcian periods. Rioult noted the long stratigraphic range of two species of *Achistrum*, but used the absence of hooks as diagnostic of the middle–upper Toarcian, even though both species extended into the Middle Jurassic. Furthermore, two of the four morphospecies used to define the middle–upper Toarcian 'zone' were only known from single specimens ('*Mortensenites*' *feifeli* and *Calclamnoidea proteus*) and a third, *Theelia vetusta*, was based on poorly preserved specimens. In addition one of the 'diagnostic' taxa for the Hettangian–Sinemurian 'zone' is simply an aggregation of *Achistrum* and *Binoculites*.
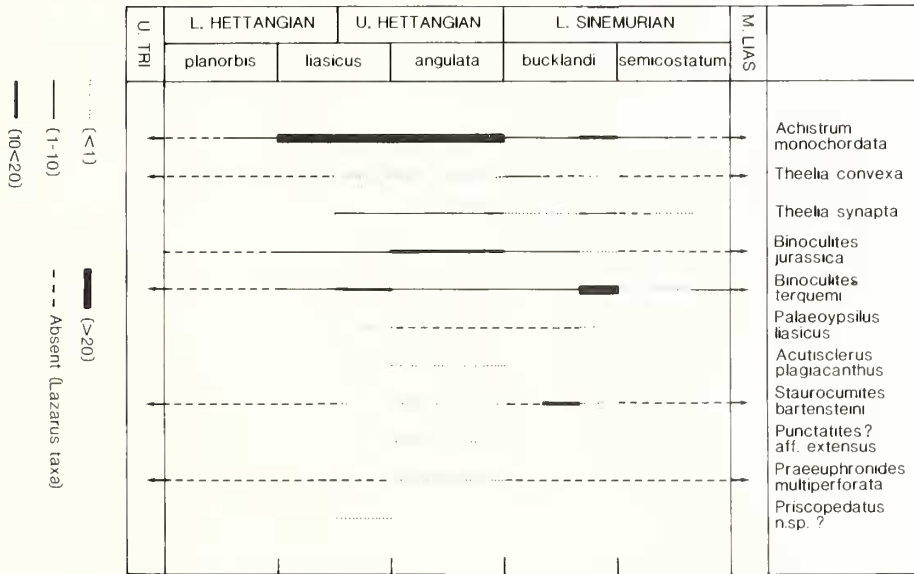
The stratigraphic distribution of the taxa recovered from the Blue Lias of southern Britain is shown in Text-figure 15 and the following changes must be made to Rioult's scheme. *Binoculites terquemi* form τ, *B. irregularis* form τ, *Ambulacrites* (= *Stichopites*) *subrectus*, *Staurocumites bartensteini* and *Theelia heptalampra* (synonymized with *T. convexa*) extend down into the Hettangian or Sinemurian and are no longer restricted to the Pliensbachian–lower Toarcian. In addition, Michelson (1972, pl. 3, fig. 5) figured a specimen of '*Calclamna germanica*' from the Hettangian identical to *Binoculites perforatus*, a morphotype previously thought to be restricted to the Pliensbachian.

These extensions of range together with taxonomic revisions result in a less well defined zonation with only the lower and middle holothurian assemblage zones of Rioult still recognizable. The biostratigraphic resolution afforded by sclerites does not compare well with that of many other fossil groups. The Hettangian–Sinemurian is characterized by *Binoculites terquemi* form β, *B. irregularis* and *B.* cf. *irregularis* (all of which are synonymous), and *Cucumarites mortenseni* and

Mortensenites circularis (both of which may not be holothurian sclerites). The fauna confined to the Pliensbachian–lower Toarcian is now reduced to *Theelia crassidentata*, *T. mortenseni*, *T. rigauda*, *Myriotrochites* (= *Stueria*)? *costifera*, and the curved rods *Ambulacrites* (= *Stichopites*) *terquemi* and *A.* (*S.*) *polymorpha* (which are probably synonymous). The Pliensbachian–lower Toarcian may also be recognized by a predominance of wide-armed *S. bartensteini* and the early growth stages of *Binoculites jurassica*.

If biostratigraphic methods other than simple presence/absence are considered, such as general abundance or bio-events, holothurians still have limited application, even on a local scale. For example, the broadly consistent sclerite composition during the Hettangian (Text-fig. 3), whilst not defining this period, may nevertheless be of some use for correlation. However, the variation in sclerite abundance and composition between sections further up the succession during the same periods of time undermines this. At present insufficient sampling also rules out the recognition of holothurian 'bio-events', such as the significant increase in *S. bartensteini* at Maisemore Cliff, although the significant percentage of wheels at Hock Cliff appears to be a local, rather than a widespread, event.

Changes within particular taxa, such as the size change in *A. monochordata* (Text-fig. 5), reveal potentially more useful biostratigraphic trends. The size change observed may even be cyclical but unfortunately there are no data from the *portlocki* zone. The relative abundance of the two *Binoculites* species also varies stratigraphically (Text-fig. 7). The Lower and lower Upper Hettangian

TEXT-FIG. 15. Stratigraphic distribution of the sclerite morphospecies found in the present study. Figures in the key are average number of sclerites per sample for each sub-zone (based on all samples). TRI, Triassic; L, Lower; M, Middle; U, Upper.

have a mixture of both *B. terquemi* and *B. jurassica*, the rest of the Hettangian (the *angulata* zone) has a preponderance of *B. jurassica* and in the Sinemurian *B. terquemi* dominates. In both cases large sample sizes are needed, which limits their application.

Evolutionary implications

Several elements of the Blue Lias holothurian fauna represent important finds with respect to the phylogeny of the class. Of particular note is the presence of *Theelia synapta*, the oldest known apodan wheel which definitely possesses the characters of a synaptid (larval) wheel. This indicates

that the lineage leading to the Synaptidae had evolved by the Lower Jurassic. The Blue Lias *Theelia convexa* are the oldest chiridotid wheels which are closely comparable with Recent forms, i.e. there is a well-developed star structure and a conservative number of spokes. The fauna includes two spired-plate morphospecies, doubling the total number known, and includes the earliest probable representative of the dactylochirote family Ypsilothuriidae. Also, although *Priscopedatus* sp. nov.? is not the earliest known four-pillared table, it is the first typical example and a morphological advance on Triassic forms.

Calcareous ring material is significant simply because of its rarity. If calcareous ring Type 1 is correctly assigned to the Molpadiida then this is the earliest record of the order, in the absence of any unequivocal molpadiid morphotypes. However, the proposed association between Type 1 and *Staurocumites bartensteini* could mean that the earliest record is the first appearance of this morphospecies, i.e. the Middle Triassic (Anisian). Type 1 elements are probably derived from Molpadiidae, indicating that this is the oldest family within the Mopadiida. The similarity of *S. bartensteini* to some dendrochirote tables, however, may indicate a close relationship between the Dendrochirotida and Molpadiida (Gilliland 1990).

Calcareous ring Type 2 is derived from an apodan and possibly a myriotrochid. The absence of associated myriotrochid morphotypes, the data in Table 1, and observations of *Achistrum*- and calcareous ring-bearing complete fossils, suggest that the 'myriotrochid-type' of ring was present in some or all apodan groups at least until the early Jurassic, i.e. the calcareous ring found in myriotrochids today is primitive.

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